University of Kansas Publications

MUSEUM OF NATURAL HISTORY

The University of Kansas Publications, Museum of Natural History, beginning with volume 1 in 1946, was discontinued with volume 20 in 1971. Shorter research papers formerly published in the above series are now published as Occasional Papers, Museum of Natural History. The Miscellaneous Publications, Museum of Natural History, began with number 1 in 1946. Longer research papers are published in that series. Monographs of the Museum of Natural History were initiated in 1970. All manuscripts are subject to critical review by intra- and extramural specialists; final acceptance is at the discretion of the publications committee.

Institutional libraries interested in exchanging publications may obtain the Occasional Papers and Miscellaneous Publications by addressing the Exchange Librarian, The University of Kansas Library, Lawrence, Kansas 66045. Individuals may purchase separate numbers of all series. Prices may be obtained upon request addressed to Publications Secretary, Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045.

Editor: E. O. Wiley
Managing Editor: Joseph T. Collins

PRINTED BY
UNIVERSITY OF KANSAS PRINTING SERVICE
LAWRENCE, KANSAS

OCCASIONAL PAPERS

of the

MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas

NUMBER 94, PAGES 1-48 NOVEMBER 5, 1981

AN ANNOTATED KEY TO THE LONG-TAILED SHREWS (GENUS *SOREX*) OF THE UNITED STATES AND CANADA, WITH NOTES ON MIDDLE AMERICAN *SOREX*

By
Jane Ann Junge[1] and Robert S. Hoffmann[2]

The long-tailed shrews are a widespread and diverse group of small mammals living in the northern parts of both hemispheres. Many species, especially the smaller members of this Holarctic genus *(Sorex),* are poorly known, since individuals are difficult to capture and even more difficult to observe.

The last complete revision of American *Sorex* (including *Microsorex,* treated here as a subgenus) was that of Jackson (1928). In the last half-century, a number of studies have clarified the systematic relationships of taxa within the genus, but these have not been compiled in a single review. Moreover, the most recent key (Hall, 1981) for the most part still reflects the species concepts of Jackson's revision, and depends heavily on geographic criteria.

In this annotated key, species are identified on the basis of skull characters, in particular those of the maxillary toothrow, since the rostral/palatal region seems to remain patent even in specimens where the skull has been badly damaged. The practical significance of basing the key on these characters is that it will permit identification of material from archeological or paleontological sites, as well as shrews damaged in capture, during preparation, or when decomposition has rendered body characters difficult or impossible to assess. The key includes new skull drawings to illustrate important characters.

[1] Curatorial Assistant, Museum of Natural History and Department of Systematics and Ecology, The University of Kansas, Lawrence, Kansas 66045.

[2] Curator of Mammals, Museum of Natural History and Professor, Department of Systematics and Ecology, The University of Kansas, Lawrence, Kansas 66045.

The notes on each species following the key describe external characteristics useful in identifying species, as well as suggestions for distinguishing among species of shrews found in the same geographic area, and relevant habitat associations. Shrews that cannot be separated readily on the basis of skull characters are seldom found in the same geographic areas (there are exceptions to this in the *Sorex cinereus* group); therefore, distribution is a useful, though not infallible, aid in identification. The range maps for each species have been redrawn from published sources to reflect current distributional records.

The superspecies concept and nomenclatural concepts advocated by Amadon (1966) are employed herein. Decisions concerning the validity of species or allospecies, although based on the published literature as noted, are the responsibility of the second author. The Middle American *Sorex* are currently under study by Hoffmann and others and are therefore omitted from this key, pending revision. These shrews are included in the comments and provisional classification. For a recent key to the Old World *Sorex* see Corbet (1978) and references cited therein.

Key Characters

Subgeneric Identification

The presence of the post-mandibular foramen is used as a character to differentiate the subgenus *Sorex* from the subgenera *Otisorex* and *Microsorex*. The mandibular canal is present in all three subgenera; its foramen is situated on the lingual side of the ramus of the jaw, the canal running forward toward the incisors. The post-mandibular foramen appears in the general vicinity of the mandibular foramen in the subgenus *Sorex*, but the post-mandibular canal runs up into the ramus of the jaw. The mandibular and post-mandibular foramina may be separated on the jaw or may be confluent in the same depression (Fig. 1). The best way to identify the post-mandibular canal is to insert a fine probe or stiff hair into the foramen. Occasionally the post-mandibular foramen and canal are absent in individuals of the subgenus *Sorex*, more frequently in some species than in others; likewise a small foramen and canal may occasionally be present in *Otisorex* shrews, at least on one side of the jaw.

A pigmented ridge runs from the apex to the cingulum on the lingual side of each unicuspid tooth (see below) of shrews in the subgenera *Otisorex* and *Microsorex*. The ridge may end in a pigmented cusplet. The presence or absence of the ridge (Fig. 2) is not highly variable and is usually the best character to use in subgeneric determinations. In some individuals, however, pigmentation of the ridge may be faint or absent, especially in the species

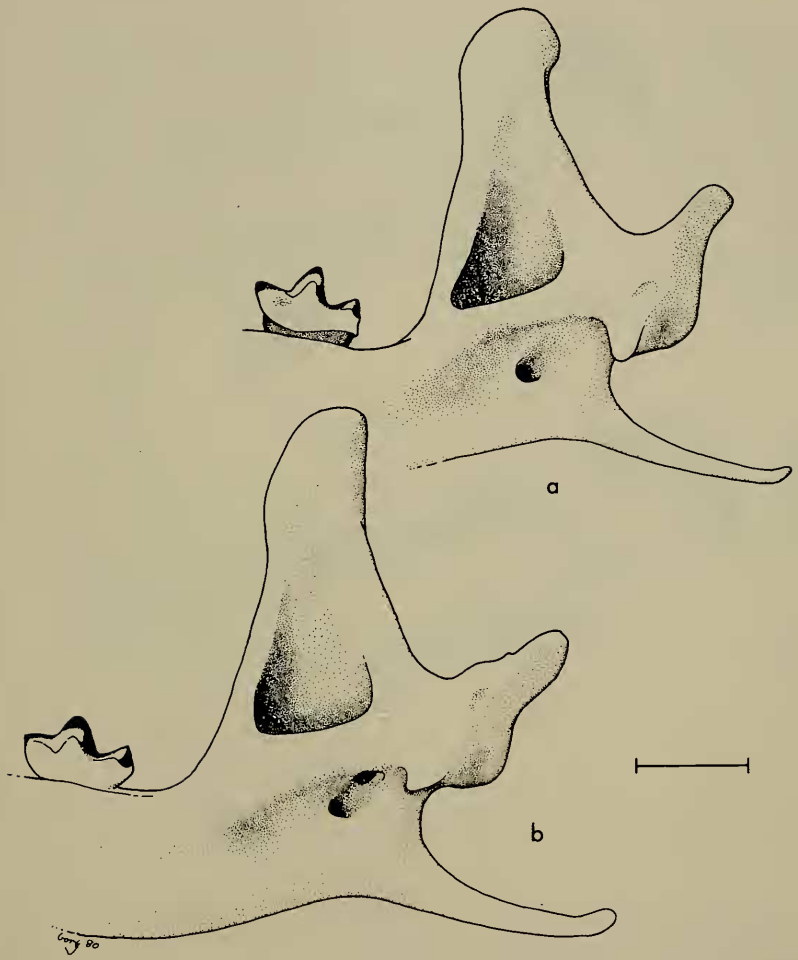

FIG. 1.—Ventro-lateral view of posterior portion of mandible showing; a) absence of post-mandibular canal characteristic of *Otisorex*, and b) presence of post-mandibular canal characteristic of *Sorex*. Bar represents 1 mm in this and subsequent figures.

fumeus, dispar, gaspensis, nanus, and *longirostris.* The distribution of these shrews is, fortunately, mostly outside that of any species of the subgenus *Sorex*.

Long considered a separate genus, *Microsorex* was reduced to subgeneric status by Diersing (1980). He considered *Microsorex* to be the most specialized member of a gradational series of *Otisorex* shrews having increasingly larger accessory tines on the antero-medial surface of the first upper incisor; at the same time the jaws become shorter, leading to a reduction in size of the third and fifth

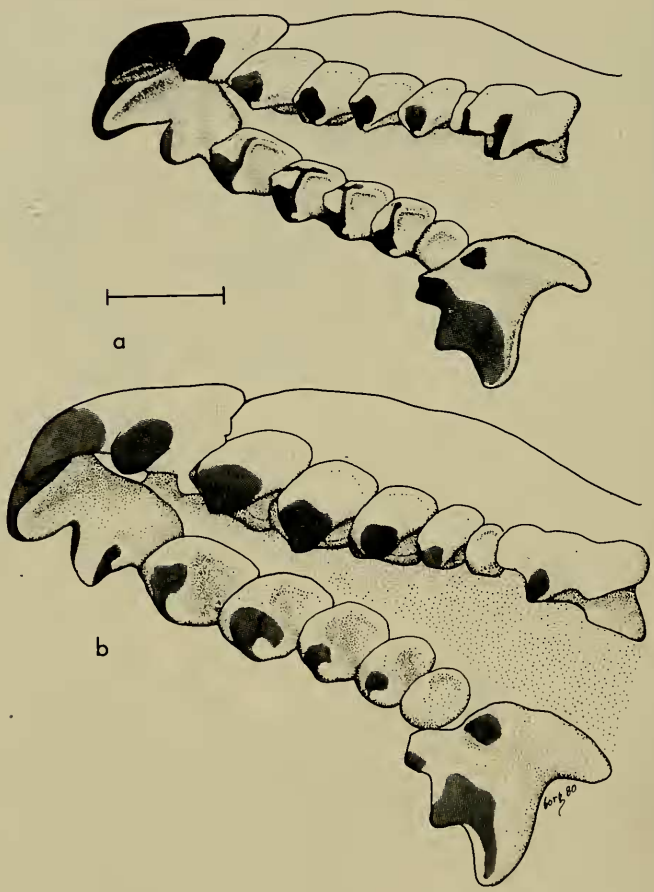

FIG. 2.—Ventro-lateral view of rostrum, showing occlusal surface of unicuspid teeth; a) pigmented ridge characteristic of *Otisorex*, and b) lack of pigmented ridge characteristic of *Sorex*.

unicuspid teeth of the maxillary row. In *Microsorex*, U3 is compressed antero-posteriorally into a tiny disc which is usually not visible in lateral view. We agree with Diersing that the reduction of U3 is not a sufficient basis to warrant generic rank (see also Repenning, 1967). The two species *thompsoni* and *hoyi* recognized by Long (1972, 1974) were synonymized under *Sorex hoyi* by Van Zyll de Jong (1976a) and Diersing (1980).

Specific Characters

Accessory medial tine of the first upper incisor (I1)

Heptner and Dolgov (1967), Yudin (1969), Hoffmann (1971), Hennings and Hoffmann (1977), and Diersing and Hoffmeister

(1977) used the antero-medial tine on the first upper incisors as a primary character in differentiating certain shrews. The presence or absence of this tine, its relative size, placement on the tooth, and the relationship of the pigmented area of the tine to that of the main pigmented area of the incisor are important characters used to discriminate between species in this key. The relative positions of tine and pigment remain constant throughout the life of the individual, becoming obscure only in old age when the incisors are extremely worn. There seems to be little individual variation of the tine within species, although it may be extremely small and difficult to find in some *(e.g., S. trowbridgii),* and absent in other species.

Unicuspid teeth

The five teeth in the maxillary toothrow following the first incisor (I1) are usually called "unicuspids" (Figs. 2, 4). The homologies of these teeth are not clear (Repenning, 1967); all are characterized by development of a single cusp, making the tooth appear conical. The unicuspids are numbered U1 through U5; the four molariform teeth behind the unicuspids are P4 through M3.

Generally, U1 and U2 are subequal in size and larger than U3 and U4. U5 is always small. U3 and U4 are seldom the same size (except in *S. dispar* and *S. gaspensis*) and their relative size is one of the characters used in this key. Occasionally there may be individuals within a species where U3 and U4 are subequal, rather than of different sizes (20% of *S. longirostris;* T. French, pers. comm.). With the possible exception of *S. cinereus ohionensis,* the size relationship is never consistently reversed within a population. The relative sizes of the unicuspids are evident throughout the lifespan of the individual until advanced old age, when excessive tooth wear may obscure the relationship.

In ventral view, the sides of the unicuspids may appear flat in some species (Fig. 23b), and relatively inflated ("bulbous"; see Choate, 1970) in others (Fig. 23a). Choate relates the degree of bulbousness of the teeth in *Cryptotis* to the hardness of food items —those species with bulbous teeth having to deal with relatively hard food items. J. S. Mellett (pers. comm.) has suggested that fibrous materials such as chitin may be more digestible if the fibers are reduced to small particle size. A more wedge-shaped tooth is more efficient in this respect. Although the relationship of tooth shape to diet in *Sorex* has not been studied, the character seems useful in making some distinctions in the key.

Skull length

Two skull length measurements are commonly used (Kirkland and Van Deusen, 1979); condylobasal length (anterior medial point

on premaxillary bones to posteriormost point on occipital condyle), and greatest length (anteriormost point on the first incisor to posteriormost point on the occipital condyle) (Fig. 3). Both are highly correlated with the overall mass and linear dimensions of the individual shrew, as well as with each other. Condylobasal length is the more difficult of the two to take, particularly on small shrews, since it requires that one point of the calipers or dividers be placed between the incisors. Greatest length, while easy to measure, is subject to more age variation since the positions of the first incisors shift, rotating downwards as the individual ages and its teeth wear down (Diersing and Hoffmeister, 1977; Diersing, 1980). The skull length measurement employed here is condylobasal (CB) length.

Skull length is useful in distinguishing between species in a single region, although interspecific geographic variation in size renders the measurement less useful as an absolute criterion. For example, where *Sorex vagrans* and *Sorex monticolus* are sympatric, the latter is the larger shrew at any one locality, even though overall there is considerable overlap in measurement (Hennings and Hoffmann, 1977). In *Sorex*, age and sex do not affect condylobasal length, so shrews, regardless of sex and extent of tooth wear, may be compared. This is not to say that variation due to age does not appear, but it is slight (Findley, 1955a; Van Zyll de Jong, 1980; Diersing, 1980).

Rostral/palatal size and proportions

The size and shape of the anterior part of the skull is also useful in differentiating species of *Sorex*. This ranges from the long, narrow rostrum of *S. dispar* (Figs. 5b, e) to the short, broad rostrum of *S. merriami* (Fig. 22a), but even superficially similar species such as *S. cinereus* and *S. haydeni* can be distinguished by their rostral/palatal proportions. Differences in proportions are best shown by either a bivariate plot or by the ratio of a width measurement against a length measurement, such as width across upper second molars versus unicuspid toothrow length (Van Zyll de Jong, 1980). Other measurements sometimes used are maxillary breadth, maxillary toothrow length, and palatal length (Fig. 3). Maxillary and unicuspid toothrow length are correlated with skull length, and may be used as an indication of size when other parts of the skull are damaged.

Interorbital breadth

While this measurement (Fig. 3) is not particularly variable between species, it may occasionally be useful. It has been used in distinguishing between *S. vagrans* and *S. monticolus* (Hennings and Hoffmann, 1977).

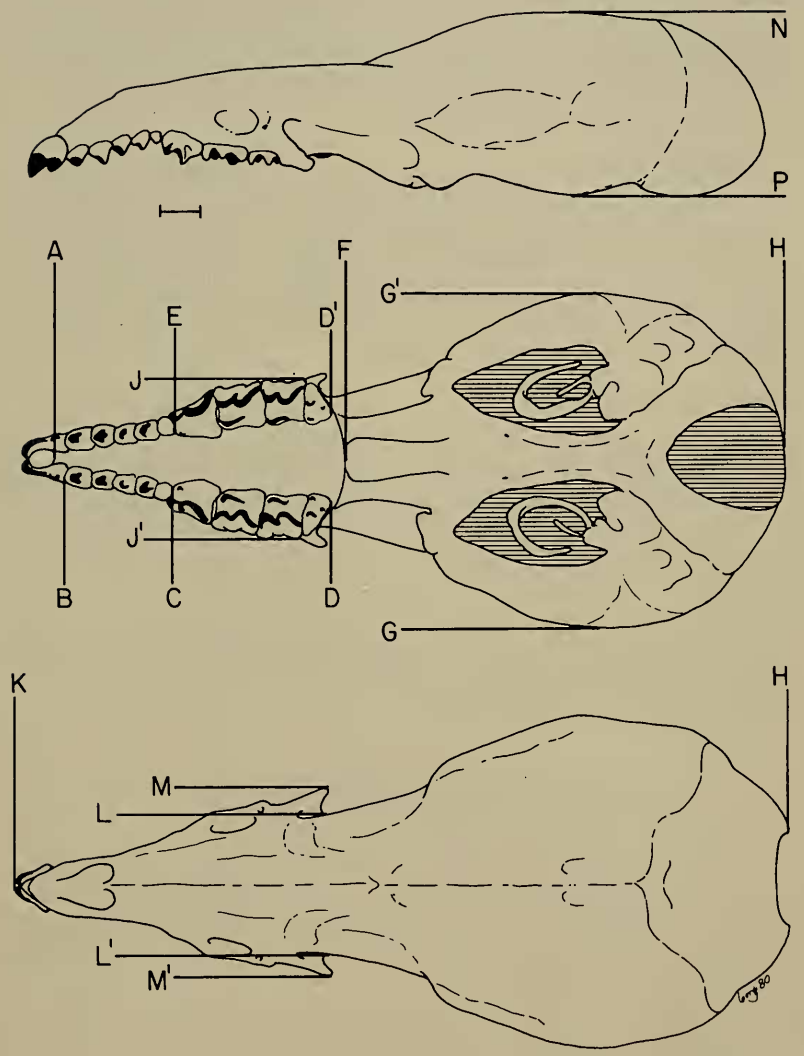

FIG. 3.—Lateral and ventral views of skull of *Sorex dispar*, showing measurements referred to in text. B-C, length of unicuspid toothrow; B-D, length of maxillary toothrow; E-D′, length of molariform toothrow; A-H, condylobasal length; K-H, greatest length of skull; K-M,M′, length of rostrum; J-J′, width of M2-M2; A-F, palatal length; G-G′, cranial breadth; N-P, cranial height; M-M′, maxillary breadth; L-L′, interorbital breadth.

Cranial breadth and height

Measurements of these dimensions (Fig. 3) are often frustrated by the fragile nature of the braincase of *Sorex*; moreover, cranial height varies with age and seasonally (Dehnel, 1949; Pucek, 1957; Dapson, 1968). Therefore, quantitative measurements of these characters have not been employed, although qualitative statements concerning relative flatness of the braincase are useful.

Zygomatic plate

The zygomatic plate comprises the outer wall of the infraorbital canal. It is bordered anteriorly by the anterior opening of the canal, posteriorly by its posterior opening and the maxillary process, and is pierced by the lacrimal foramen. The position of the anterior border of the plate and of the lacrimal foramen relative to the first and second upper molar teeth is sometimes a useful taxonomic character (Van Zyll de Jong, 1980).

External measurements

The external measurements usually taken on shrews are total length, length of tail, and length of hind foot. Since this key is based on cranial characters, other measurements are mentioned only in the notes on each species. Another reason for avoiding external measurements is that in such small animals, subject to rapid decomposition and deformation in the measuring process, it is difficult to make accurate measurements, particularly of total length. Since skull or toothrow (see above) lengths are correlated with external linear dimensions and can be measured more accurately, they are preferred as an indication of size.

Key to the Long-tailed Shrews (Genus Sorex) of the United States and Canada

1. Usually no post-mandibular foramen (Fig. 1a); or, if present, small and often only on one mandible. Unicuspids with a ridge, usually pigmented, on the lingual face, running from apex to cingulum, sometimes ending in a pigmented cusplet (Fig. 2a). 2

1a. Usually a well-developed post-mandibular foramen (Fig. 1b). No pigmented ridge on lingual face of the unicuspids (Fig. 2b). Subgenus *Sorex* 22

2. Unicuspid toothrow "crowded," only three unicuspids easily visible in lateral (buccal) view (Fig. 4a); U3 tiny, disc-like; U4 of normal size and shape; U5 minute (Fig. 4b). Accessory medial tine on anterior surface of first upper in-

cisor (I1) relatively large and long (Fig. 4c). Condylobasal (CB) length 12.7-15.8 mm. Distribution, boreal and montane (Fig. 24). Subgenus *Microsorex* ..... *Sorex hoyi* (p. 25)

2a. Four or five unicuspids visible from side; U3 equal to or larger than U4 (Fig. 5a), or if smaller, of normal shape rather than disc-like (Fig. 6a). Medial tine, if present, not as above (Figs. 6b, 7b, 9). Subgenus *Otisorex* 3

3. U3 and U4 usually equal in size (Fig. 5a, b), or if different, U3 slightly smaller; anterior edge of zygomatic plate posterior to plane separating M1 and M2 (Fig. 5a); rostrum unusually long and narrow, cranium flattened. Unicuspids widely spaced, relatively narrow (Fig. 5b, c); ridge on lingual face of unicuspids often lacking pigment (Fig. 5c). *Sorex dispar* group 4

3a. Not as above 5

4. Skull larger, CB length 16.5-18.4 mm. Distributed in upland areas in a narrow belt running along the Appalachian Mountains from Maine to North Carolina, with an isolated population in New Brunswick, Canada (Fig. 25). ..... *Sorex dispar* (p. 25)

4a. Skull smaller, CB length 15.4-16.4 mm. Distribution, Gaspé Peninsula, northern New Brunswick, and Cape Breton Is. (Fig. 25). ..... *Sorex gaspensis* (p. 27)

5. U3 usually distinctly smaller than U4 (Figs. 6a; 7a; 12a, b; 14a, b), sometimes subequal 6

5a. U3 usually larger than U4, sometimes subequal (Figs. 15a, 16a, 17a, 18, 19). *Sorex fumeus* and *cinereus* groups 14

6. Skull large, CB length usually more than 19.0 mm. 7

6a. Skull medium to small, CB length usually less than 19.0 mm. 9

7. Largest North American *Sorex*, CB length 20.8-23.8 mm; skull and teeth robust; rostrum relatively long, broad, distinctly downcurved (Fig. 6a); medial tine may be large, placed high on face of I1, pigmented; pigmented area of incisor may curve up to meet that of tine. Distribution, northwest Pacific coast (Fig. 24). ..... *Sorex bendirii* (p. 28)

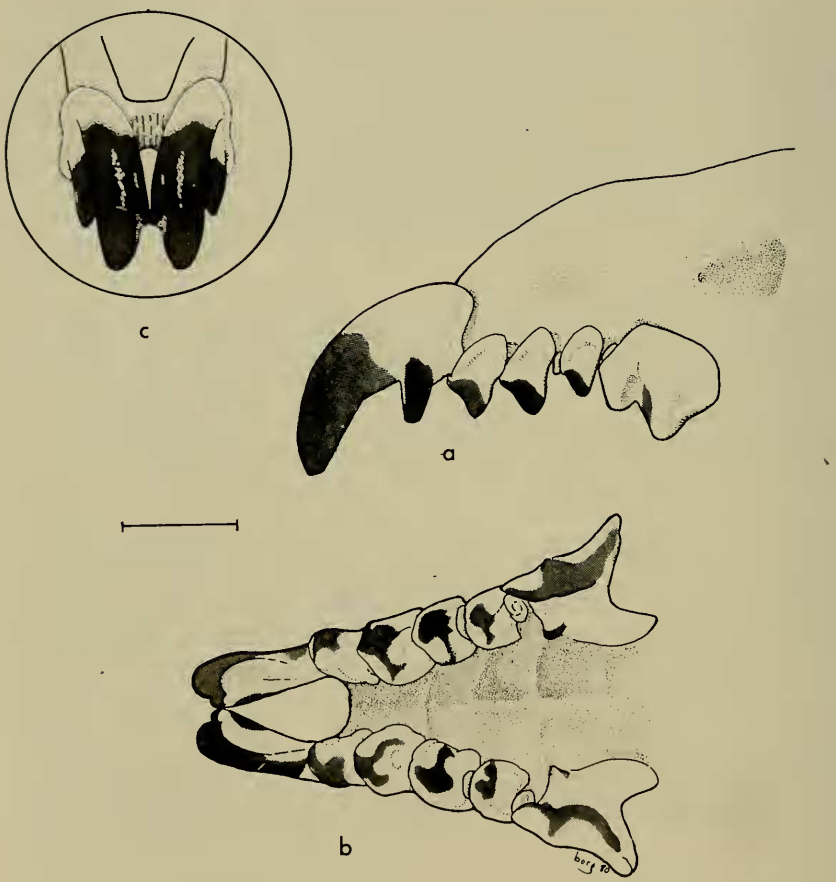

FIG. 4.—*Sorex hoyi;* a) lateral (buccal) view of unicuspid toothrow, b) ventral view, showing U1, U2, U4, and tiny U3 and U5, and c) frontal view of first incisor.

7a. Medial tine absent or, if present, small and placed low on medial face of I1 (Fig. 7b); somewhat smaller, CB length 19.0-22.8 mm; skull and teeth not so robust, rostrum not downcurved (Fig. 7a). 8

8. Small medial tines present on I1 (Fig. 7b); unicuspids longer than wide in ventral view (Fig. 8a). Distribution, boreo-montane (Fig. 26). ..... *Sorex palustris* (incl. *alaskanus*) (p. 28)

8a. No medial tines present on I1 (as in Fig. 21b); unicuspids wider than long to approximately quadrate in ventral view (Fig. 8b). Distribution, Pacific coast from San Francisco Bay north to central Oregon (Fig. 27). ..... *Sorex pacificus* (p. 28)

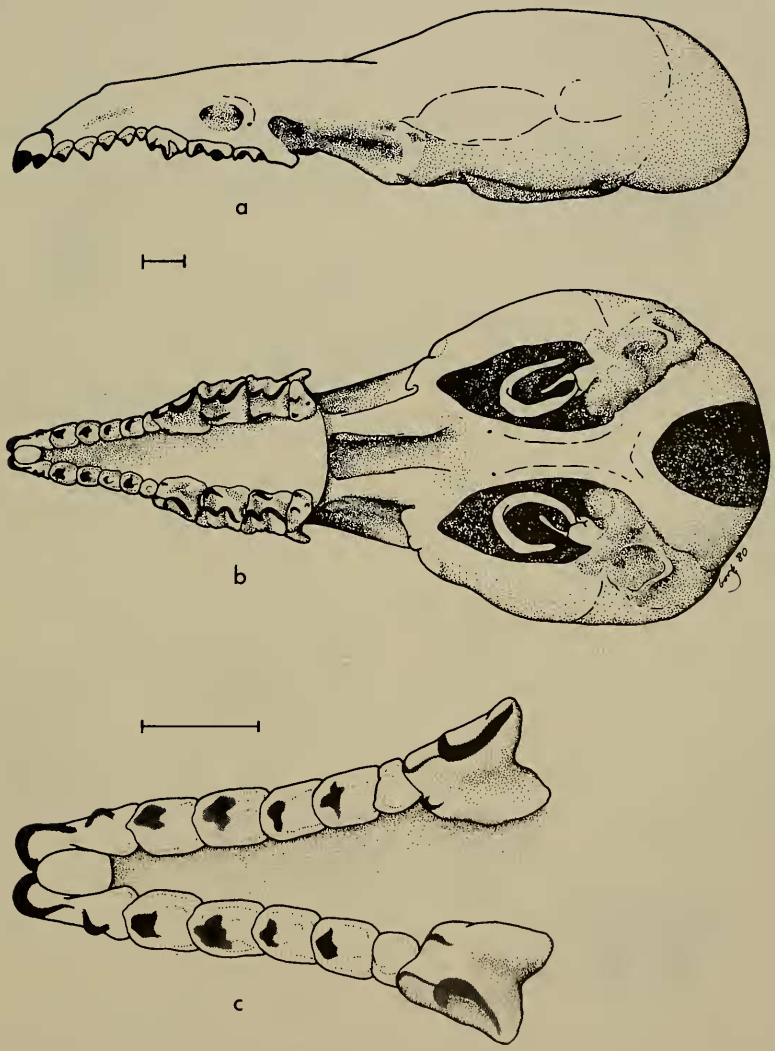

FIG. 5.—*Sorex dispar;* a) lateral view of skull, b) ventral view of skull, and c) ventral view showing occlusal surface of upper unicuspids.

9. Medial tine begins above main pigmented area of first incisor (Figs. 9a, b). 10

9a. Medial tine contained entirely within pigmented area of first incisor (Fig. 9c). 11

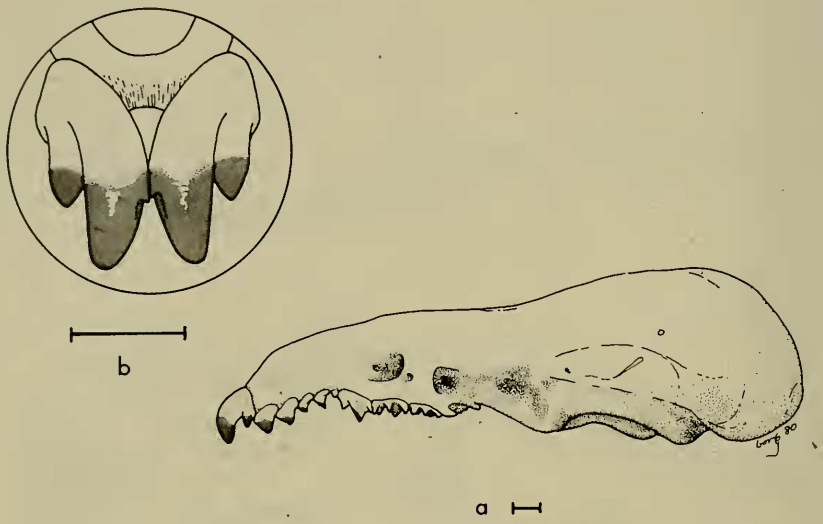

FIG. 6.—*Sorex bendirii;* a) lateral view of skull, and b) frontal view of first incisor.

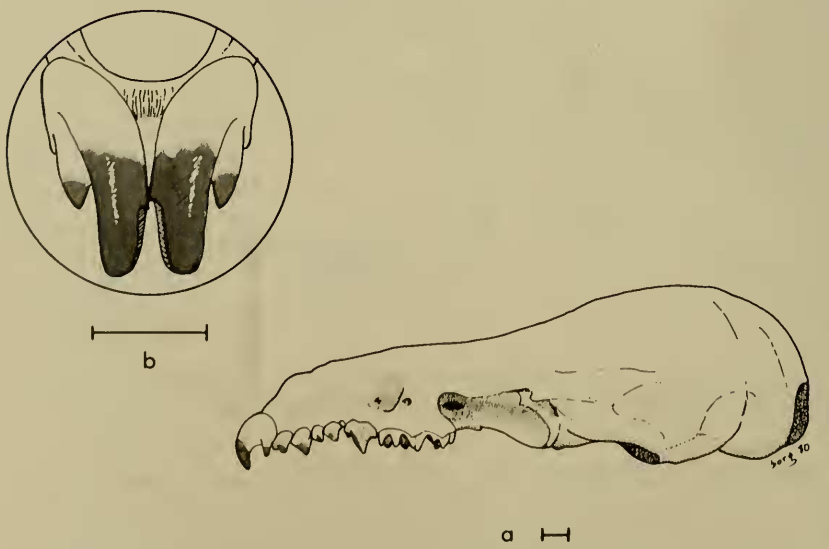

FIG. 7.—*Sorex palustris;* a) lateral view of skull, and b) frontal view of first incisor.

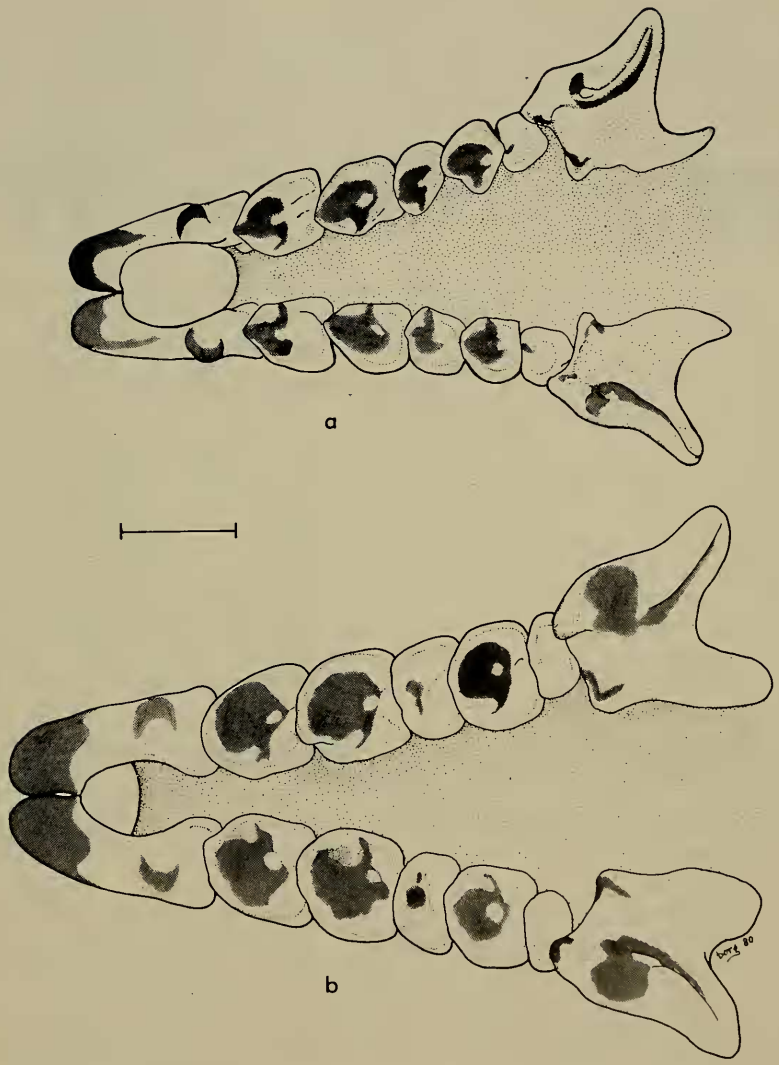

FIG. 8.—Ventral view of upper unicuspids of a) *Sorex palustris,* and b) *Sorex pacificus.*

10. Skull larger, CB length 15.5-17.5 mm. Usually distinct unpigmented gap between upper pigmented area of first incisor and pigmented medial tine (Fig. 9a). Rostrum relatively long and narrow, cranium relatively inflated. Unicuspids quadrate or longer than wide; U1 and U2 more robust, bulbous; U3 definitely smaller than U4. Distribution, western North America (Fig. 28). ..... *Sorex vagrans* (p. 31)

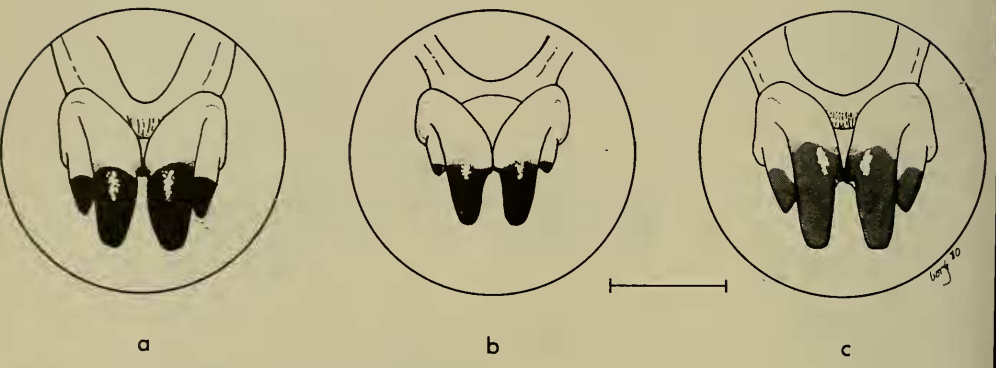

FIG. 9.—Frontal view of first incisors of a) *Sorex vagrans,* b) *Sorex longirostris,* and c) *Sorex monticolus.*

10a. Skull smaller, CB length 13.8-15.6 mm (except S. *l. fisheri,* 15.4-16.4 mm). Usually no definite gap between pigmented areas of incisor and medial tine (Fig. 9b). Rostrum relatively short and broad, cranium relatively flat (Fig. 10). Unicuspids wider than long; U1 and U2 less robust, not bulbous; U3 and U4 sometimes subequal. Distribution, southeastern North America (Fig. 28). ..... *Sorex longirostris* (p. 33)

11. CB length 15.4 mm or more; in ventral view, U3 usually distinctly smaller than U4 (Figs. 12, 13a). 12

11a. CB length 15.3 mm or less; U3 and U4 may sometimes appear subequal in ventral view (Fig. 13b). 13

12. CB length 16.1-19.2 mm; cranium relatively inflated (Fig. 11a). Unicuspids become appressed posteriorly, U5 against P4, with no noticeable gap between U5 and P4 along medial edge (Fig. 12a). Distribution, northwestern montane and boreal North America (mostly north and east of S. *ornatus*) (Fig. 27). ..... *Sorex monticolus* (p. 33)

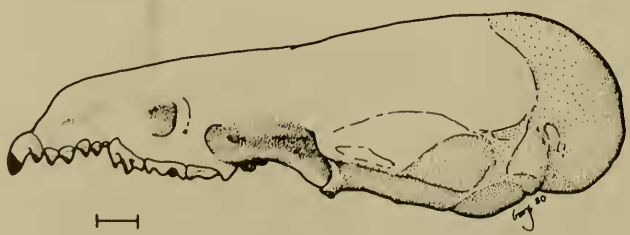

FIG. 10.—Lateral view of skull of *Sorex longirostris.*

12a. CB length 15.4-17.0 mm; cranium relatively flat (Fig. 11b). Unicuspid toothrow less appressed posteriorly, so that there is a distinct triangular gap between U5 and P4 along the medial edge (Figs. 12b, 13a). Distribution, California, south from the San Francisco Bay area, west of the crest of the Sierra Nevada, Santa Catalina Island, and Baja California (mostly south and west of *S. monticolus*) (Fig. 24). ---- *Sorex ornatus* (incl. *S. sinuosus, S. willeti, S. juncensis*) (p. 34)

13. CB length 13.8-14.8 mm; cranium extremely flat (Fig. 14a). Distribution, discontinuous, mostly montane, in Rocky Mountains, Colorado Plateau, and western Great Plains (Fig. 25). ---------- *Sorex nanus* (p. 35)

13a. CB length 14.5-15.3 mm; cranium less flat (Fig. 14b). Distribution, southern Great Basin (Fig. 25). ---------- ---------- *Sorex tenellus* (p. 35)

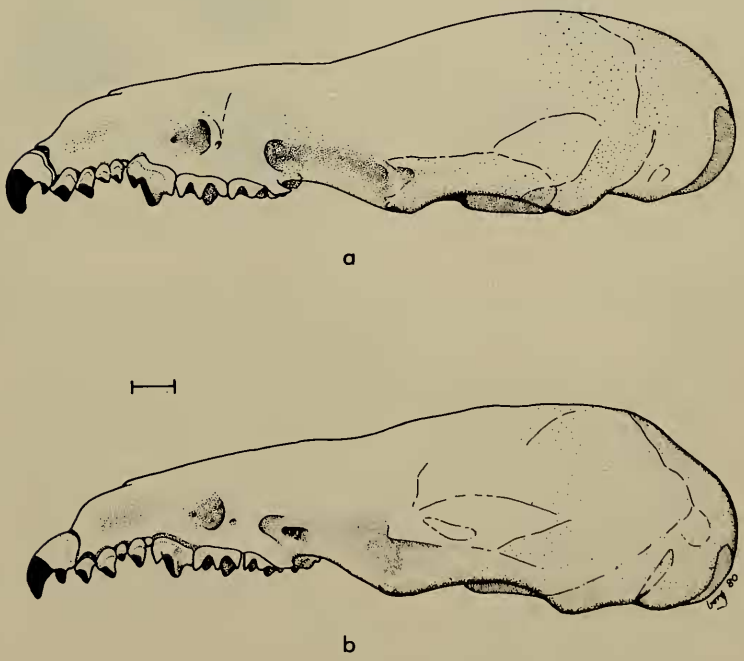

FIG. 11.—Lateral view of skulls of a) *Sorex monticolus,* and b) *Sorex ornatus.*

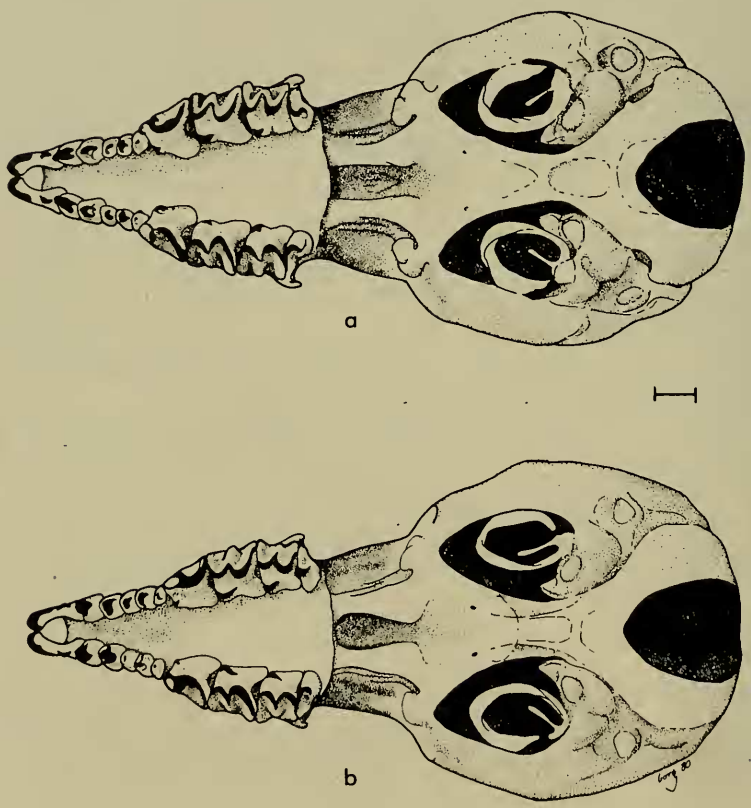

FIG. 12.—Ventral view of skulls of a) *Sorex monticolus,* and b) *Sorex ornatus.*

14. Skull large, CB length 17.8-19.0 mm; palate broad; maxillary breadth greater than 4.6 mm; cranium usually flattened to some degree, sometimes extremely so (Fig. 15a). Unicuspids wider than long; ridge on lingual face of unicuspid often lacking pigment (Fig. 15b). Small post-mandibular foramen sometimes present, at least on one mandible. Distribution, northeastern United States and southeastern Canada (Fig. 31). ..... *Sorex fumeus* (p. 35)

14a. Skull small to moderate, CB length 13.8-17.0 mm, the larger species with inflated braincase (Fig. 16a). Maxillary breadth less than 4.6 mm; unicuspids relatively narrow, quadrate to longer than wide (Fig. 16b). *Sorex cinereus* group 15

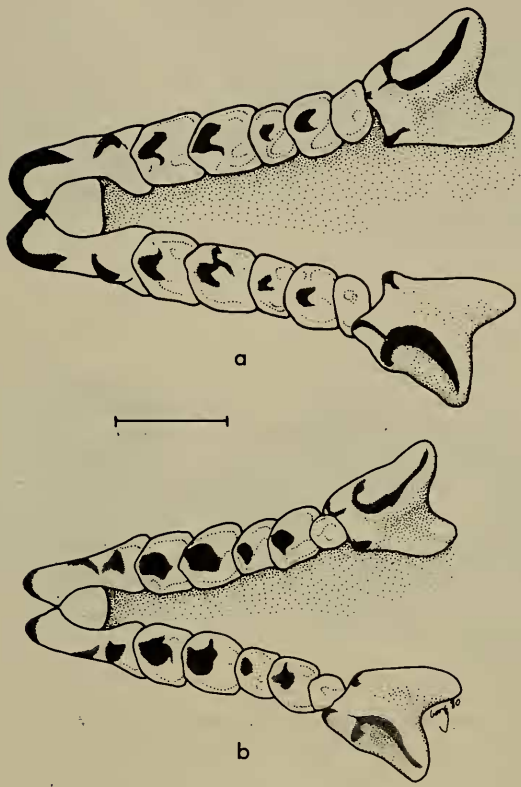

FIG. 13.—Ventral view of upper unicuspids of a) *Sorex ornatus,* and b) *Sorex nanus.*

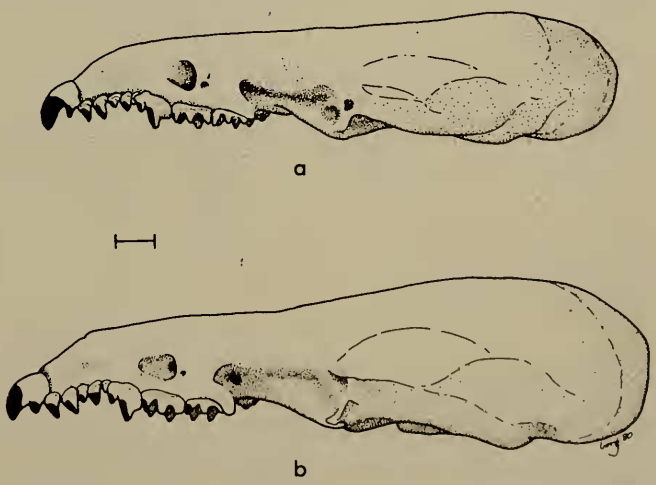

FIG. 14.—Lateral view of skulls of a) *Sorex nanus,* and b) *Sorex tenellus.*

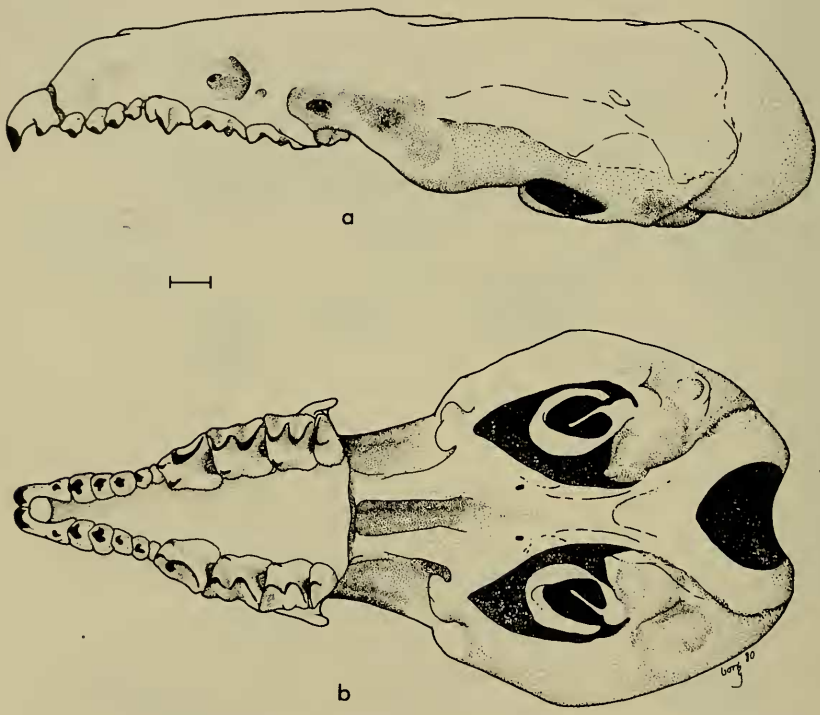

FIG. 15.—*Sorex fumeus;* a) lateral view of skull, and b) ventral view of skull.

15. Extremely small, CB length 13.8-14.6 mm, skull relatively flat. Unicuspid teeth closely appressed, rostrum relatively short (Fig. 17a, b). When sympatric with *S. cinereus* and *S. haydeni* (see below), this is the smaller shrew. Distribution, Columbia Plateau to western Great Plains (Fig. 29). ..... *Sorex preblei* (p. 35)

15a. Usually larger, CB length usually 14.6-17.0 mm (but to 14.1 mm in some populations, see below); unicuspids well-spaced; rostrum relatively more elongate (Figs. 16, 18). 16

16. Found only on islands in Bering Strait or Sea. 17

16a. Not as above. 18

17. Known only from St. Paul, Pribilof Islands (Fig. 30). (Report from Unalaska probably in error.) ..... *Sorex hydrodromus* (incl. *S. pribilofensis*) (p. 36)

17a. Known only from St. Lawrence Island (Fig. 30). ..... *Sorex jacksoni* (p. 36)

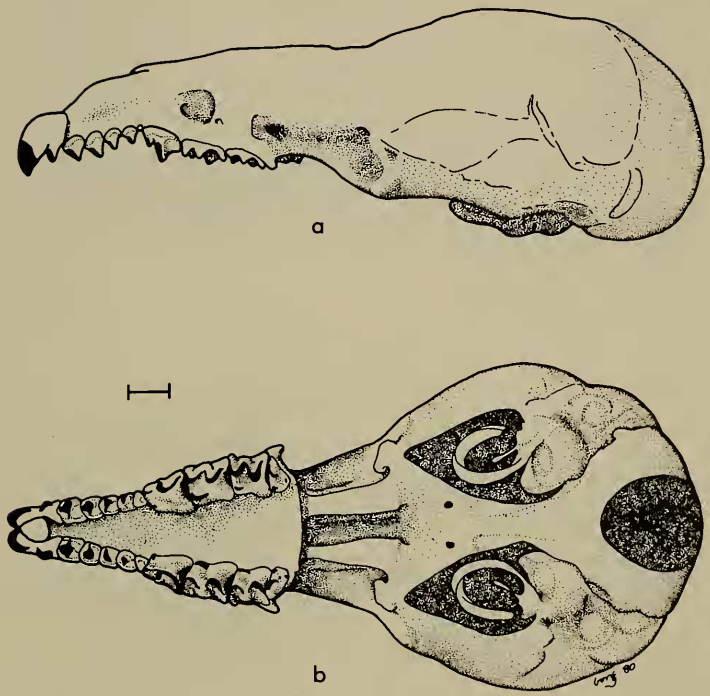

FIG. 16.—*Sorex cinereus;* a) lateral view of skull, and b) ventral view of skull.

18. Usually smaller, CB length 14.1-15.6 mm; unicuspid toothrow relatively shorter, M2-M2 width relatively larger; ratio of length of unicuspid toothrow to M2-M2 width usually less than 0.6 (Fig. 18b). 19

18a. Usually larger, CB length 14.6-17.0 mm; unicuspid toothrow relatively longer, width of M2-M2 relatively smaller; ratio of unicuspid toothrow length to M2-M2 width usually greater than 0.6 (Fig. 16b). 20

19. Restricted to northern Great Plains area, south of 55 degrees N Latitude (Fig. 30). ..... *Sorex haydeni* (p. 36)

19a. Restricted to tundra of extreme northwestern North America, north of 58 degrees N Latitude (Fig. 30). ..... *Sorex cinereus* (in part) (p. 39)

20. CB length 14.6-15.2 mm; cranium relatively flat; rostrum broad, and unicuspid toothrow slightly shorter (Fig. 19). Distribution, southern Pennsylvania, Delaware, Maryland, northeastern Virginia (Fig. 30). ..... *Sorex fontinalis* (p. 38)

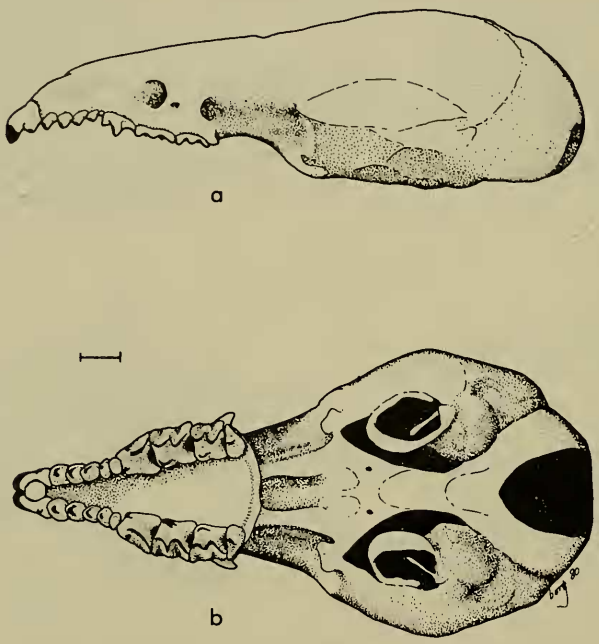

FIG. 17.—*Sorex preblei;* a) lateral view of skull, and b) ventral view of skull.

20a. CB length 15.0-17.0 mm; cranium inflated; rostrum narrow, and unicuspid toothrow slightly longer (Fig. 16a, b). 21

21. Found only in central Sierra Nevada (Fig. 30). ..... *Sorex lyelli* (p. 39)

21a. Found throughout much of northern and middle latitudes of North America (Fig. 30). ... *Sorex cinereus* (in part) (p. 39)

22. U3 usually smaller than U4 (Fig. 20a). Small medial tine high on anterior face of I1 (Fig. 20b). Distribution, Pacific Coast (Fig. 31). ..... *Sorex trowbridgii* (p. 40)

22a. U3 usually larger than U4 (Figs. 21a, 22, 23). 23

23. No medial tine on anterior face of I1 (Fig. 21b). Palate unusually broad (Fig. 22a); CB length 15.0-16.6 mm. Distribution, Columbia Plateau and Great Basin to western Great Plains (Fig. 31). ..... *Sorex merriami* (p. 40)

23a. Medial tine on anterior face of I1 (as in Fig. 20); palate not unusually broad (Fig. 22b). 24

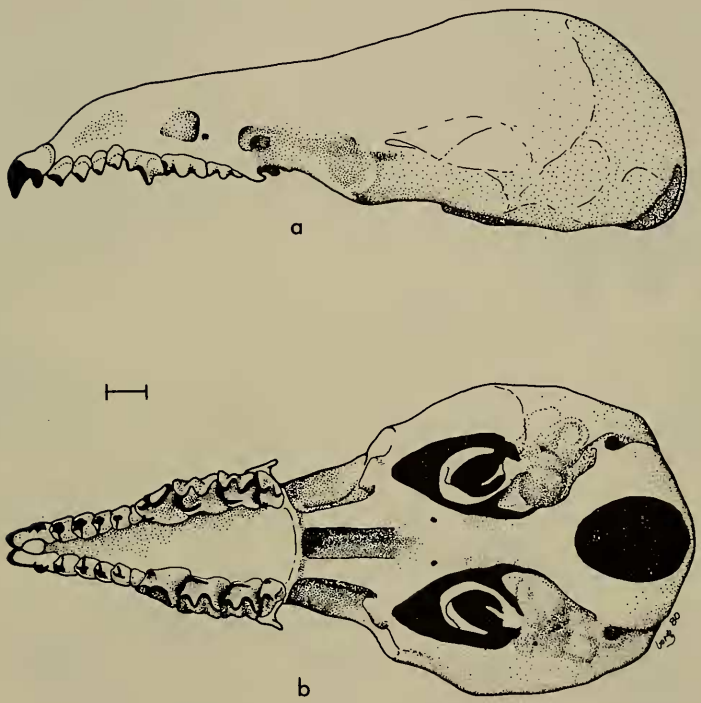

FIG. 18.—*Sorex haydeni;* a) lateral view of skull, and b) ventral view of skull.

FIG. 19.—Lateral view of skull of *Sorex fontinalis.*

24. CB length 16.5 mm or less, maxillary toothrow 6.0-6.4 mm (Fig. 22b). Described only from mountains of Arizona, New Mexico, and adjacent Mexico (Fig. 31). ..... *Sorex arizonae* (p. 42)

24a. Skull length 17.0 mm or more; maxillary toothrow 6.0-7.8 mm. Found in upper Great Lakes, northeastern Great Plains, Canada, and Alaska (Fig. 29). *Sorex arcticus* group 25

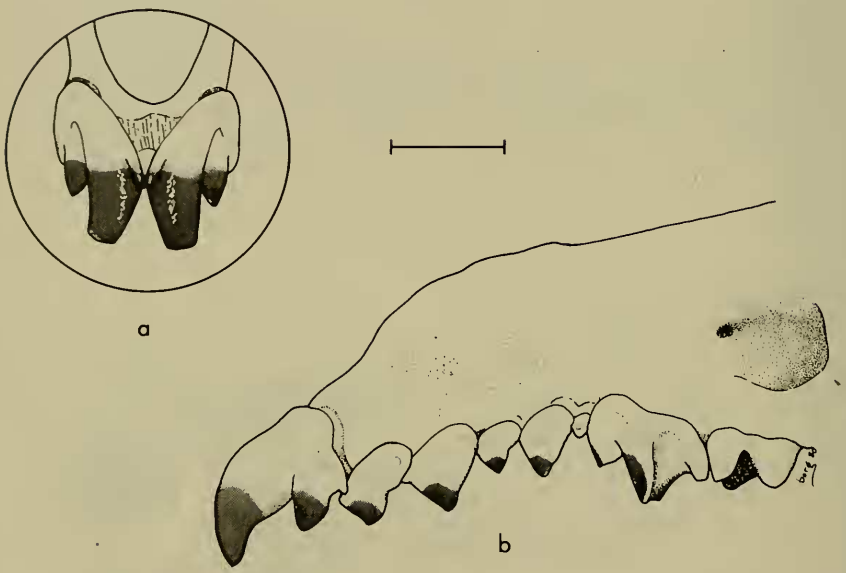

FIG. 20.—*Sorex trowbridgii;* a) lateral view of rostrum and unicuspids, and b) frontal view of first incisor.

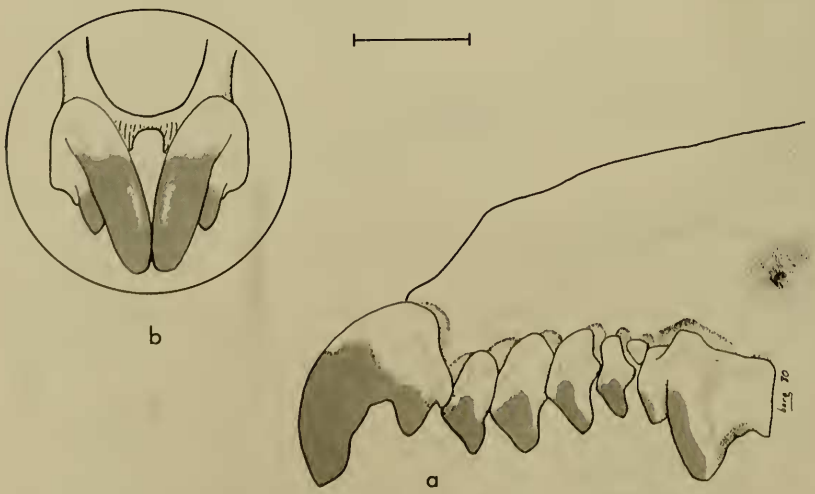

FIG. 21.—*Sorex merriami;* a) lateral view of upper unicuspids and b) frontal view of first incisor.

25. CB length 18.3-20.3 mm; maxillary toothrow 6.8-7.8 mm. Unicuspid row appears uncrowded; unicuspids robust and appear bulbous in ventral view (Fig. 23a). Distribution, upper Great Lakes, northeastern Great Plains, and Canada, except NW Yukon and extreme NW British Columbia (Fig. 29). ..... *Sorex arcticus* (p. 42)

25a. CB length 17.0-18.5 mm; maxillary toothrow 6.0-6.9 mm. Unicuspids appear crowded, less robust, not bulbous (Fig. 23b). Distribution, Alaska, Yukon, and extreme NW British Columbia (Fig. 29). ..... *Sorex tundrensis* (p. 42)

DISCUSSION

With very few exceptions (*e.g.*, *S. fontinalis*, *S. lyelli*, *S. arizonae*, and the insular species, *S. hydrodromus* and *S. jacksoni*), shrews occupy broad geographic areas. Certain regions, especially the Pacific Coast, may support a bewildering assortment of sym-

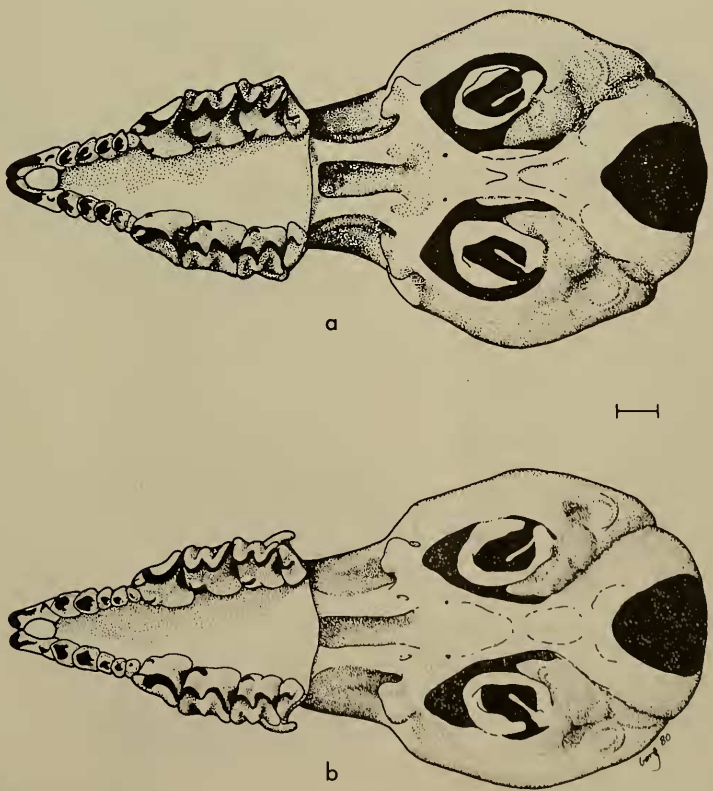

FIG. 22.—Ventral view of skulls of a) *Sorex merriami*, and b) *Sorex arizonae*.

patric or parapatric shrews. Although most species key out entirely on the basis of skull characters, occasionally reference must be made to the distribution of a species. Distribution maps have been provided for each of the species in the key as well as for the Middle American species discussed below. As far as possible, maps have been drawn from current sources; all are to the same scale and are bipolar oblique conic conformal projections.

Three groups, *S. hoyi*, *S. palustris*, and the *S. cinereus* complex *(cinereus, haydeni, preblei, fontinalis)* are extremely wide-ranging, coming in contact in one part or other of their ranges with many other species of *Sorex*. The very small *S. hoyi*, with its unique disc-shaped U3, and the large *S. palustris*, with its fringed hind feet and distinctive pelage color, are readily distinguished from other *Sorex*

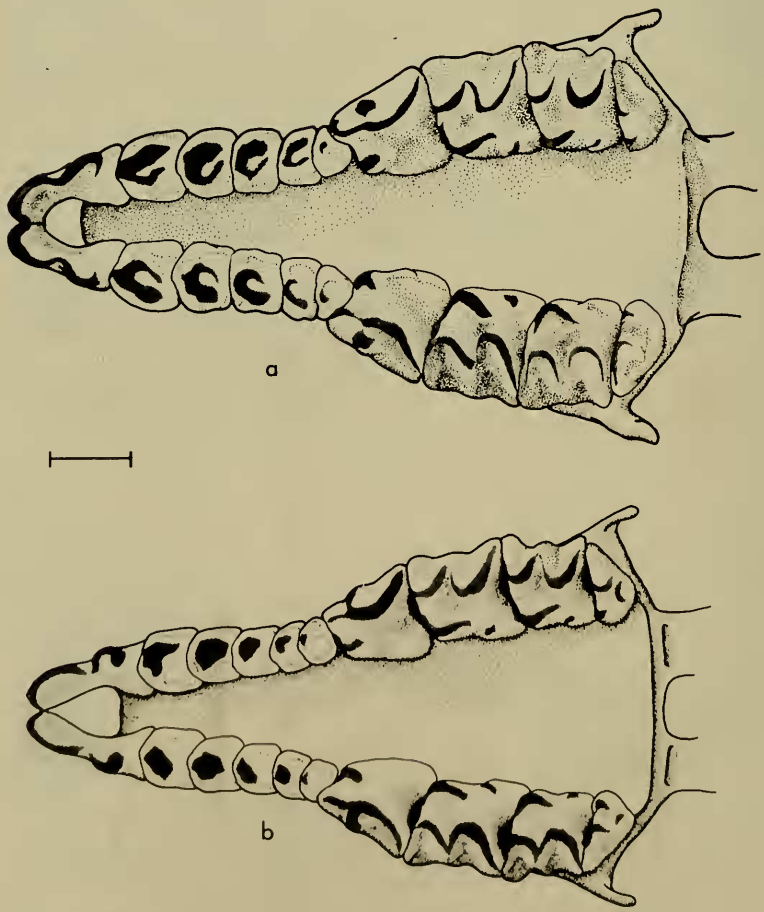

Fig. 23.—Ventral view of palates of a) *Sorex arcticus*, and b) *Sorex tundrensis*.

inhabiting the same range. Notes on how to distinguish members of the more generalized S. *cinereus* complex from other sympatric *Sorex,* as well as from each other, are given in the detailed comments on each species below. Generally, however, shrews which live in the same geographic area are quite different in cranial characteristics, while those of similar morphology occupy different ranges.

Systematic questions involving "salt-marsh melanism" in S. *vagrans* and S. *ornatus* in the San Francisco Bay area are discussed under S. *ornatus.* Relationships of the Mexican and Guatemalan *Sorex* are unclear, while those of S. *tundrensis* and the Palearctic "S. *arcticus*" are being examined by the authors and others. The systematic and nomenclatural problems associated with *Sorex pribilofensis* are discussed under S. *hydrodromus.*

Comments on the Species of North and Middle American *Sorex*

Species are listed in the following section in the same order as they appear in the key, followed by the Middle American species that are not included in the key. Annotation consists of brief notes on habitat, means by which species can be distinguished from one another in areas of sympatry, and comments on systematic status. Once a specimen is keyed out, its identity can be checked by reference to these notes.

Subgenus *Microsorex*

Pygmy Shrew *(Sorex hoyi).* The pygmy shrew is a widespread inhabitant of the northern coniferous forest or taiga, with southern outliers in the montane forests of the Appalachian and Rocky mountains. It seems to be the smallest long-tailed shrew in any one locality, although S. *nanus* may be nearly as small where both occur in the Rocky Mountains of Wyoming and Colorado (Figs. 24, 25). The pygmy shrew can be distinguished from all other North American *Sorex* by its small disc-like U3 and the long medial tine on I1. Formerly considered a monotypic genus, *Microsorex* was reduced to subgeneric status by Diersing (1980) (see above, pg. 3).

Subgenus *Otisorex*

Rock Shrew *(Sorex dispar).* This and the related Gaspé shrew (see below) have distinctive long unicolored tails (80-90% of head/body length; Kirkland, 1981) and long narrow rostra. S. *dispar* shares the southern part of its range (Fig. 25) with the smaller S. *hoyi,* S. *longirostris,* S. *fontinalis,* and S. *cinereus,* as well as the larger S. *palustris.* The only species it is likely to be confused with is S. *fumeus* which is similar in size to *dispar,* though slightly larger than *gaspensis,* and similar to both in color, especially in winter

pelage. *S. fumeus* has a shorter, bicolored tail and a broad rostrum and palate, distinctly different from the long narrow rostra and palates of *S. dispar* and *S. gaspensis*. While the unicuspids of *dispar* and *gaspensis* have the characteristic *Otisorex* ridge from apex to cingulum, in some specimens it is only lightly pigmented or not at all, and may superficially resemble the condition of subgenus *Sorex*.

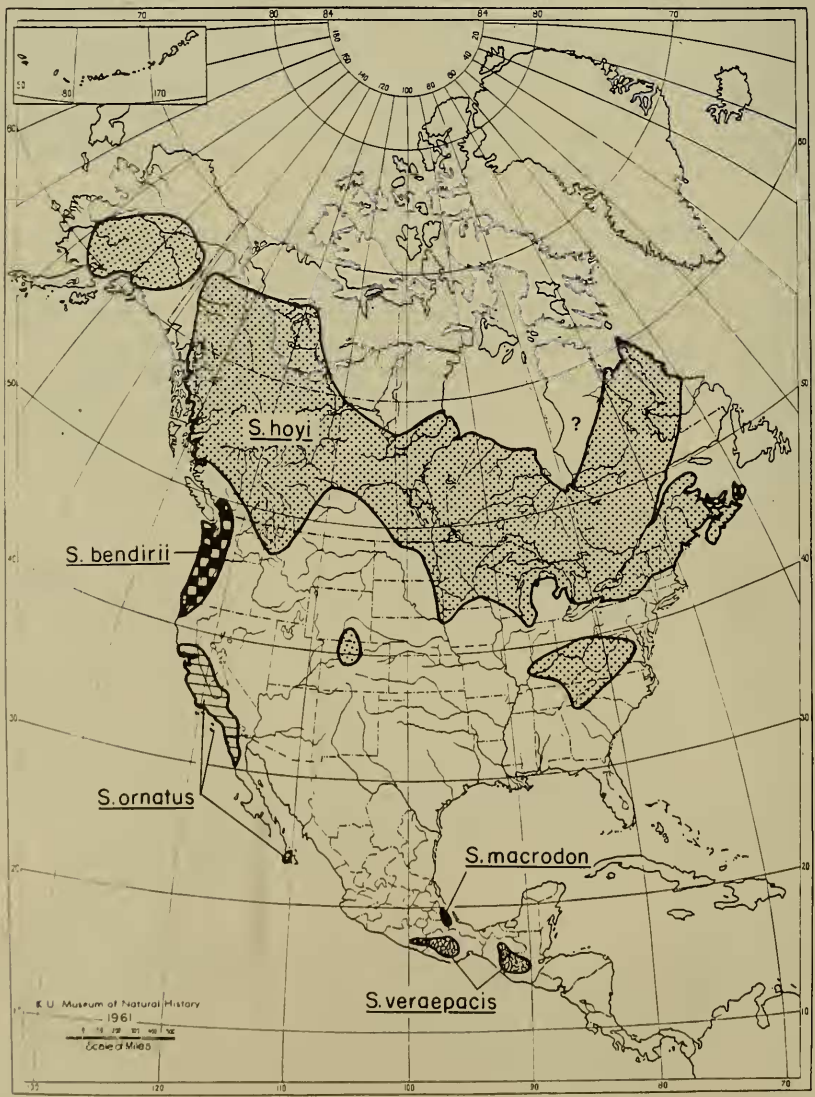

FIG. 24.—Distribution of *Sorex hoyi, Sorex bendirii, Sorex ornatus, Sorex veraepacis,* and *Sorex macrodon.*

These shrews are, as their name implies, most commonly found in rocky areas such as talus slopes and along streams (Kirkland, 1981).

Gaspé Shrew *(Sorex gaspensis).* Although very similar to *S. dispar* in characters and habitat, this species is smaller, and the ranges of the two forms are not known to meet (Fig. 25). For comparisons with other species, see *S. dispar.*

FIG. 25.—Distribution of *Sorex dispar, Sorex gaspensis, Sorex nanus,* and *Sorex tenellus.*

Marsh Shrew *(Sorex bendirii.)* This is the largest species of *Sorex* in North Ameriea. It is restricted to the northwestern Pacific eoastal region (Fig. 24) where it inhabits the forest floor in damp to wet forests, often along the banks of streams and ponds. It enters the water freely, but does not possess the dense fringe of hairs on the margins of the hind feet that adapt the water shrew *(S. palustris)* to swimming and diving. Both species oeeur in the Olympic Mountains of northwestern Washington and the Caseades of southwestern British Columbia, Washington, and Oregon, but only *S. bendirii* is known from the Coast Ranges, south to extreme northern California. The marsh shrew may be distinguished from the water shrew by its generally larger size (there is some overlap), relatively longer, more robust downeurved rostrum, and large medial tine on I1 (Fig. 6). The dorsal eolor of *S. bendirii* is blaekish, and the belly is blaek to brownish gray, unlike most *S. palustris*. *S. pacificus* (see below), whieh also occurs from central Oregon southward, differs in possessing no medial ineisor tines, and is einnamon-brown in eolor. *S. bendirii* also oeeurs with *S. trowbridgii*, a subgenus *Sorex* shrew with large post-mandibular foramina; and *S. vagrans*, from whieh it may be distinguished by size and ineisor tine pattern. In the northern parts of its range *S. bendirii* oeeurs with the smaller *S. monticolus* and *S. cinereus*.

Water Shrew *(Sorex palustris)*. Second only to the marsh shrew in size, this speeies is the largest *Sorex* throughout mueh of its range. It is boreomontane in distribution, oeeurring throughout most of the boreal taiga and southward into the Sierra Nevada, Roeky, and Appalaehian mountains (Fig. 26). It is usually elosely restricted to the vicinity of streams and ponds, and is the most aquatie member of the genus. It oeeurs with three subgenus *Sorex* shrews; the usually trieolored *S. arcticus* and *S. tundrensis* in the northern parts of its range, as well as with the coneolor *S. trowbridgii* on the Paeific Coast. Its large size, fringed hind feet, and distinctive eolor (black dorsally, with a "frosting" of light hairs; silvery-white to grayish below, exeept in the northeastern U.S. and on Vancouver Island, where populations with dark brownish venters occur) distinguish it from all other *Otisorex* shrews that may occur with it. These ineludc *S. cinereus*, *S. hoyi*, and *S. monticolus* in the northern part of the range; *S. fumeus*, *S. dispar*, *S. gaspensis*, *S. fontinalis*, and *S. longirostris* in the Appalaehians; and *S. nanus*, *S. vagrans*, *S. lyelli*, *S. preblei*, and *S. haydeni* in the Sierra and Rockies. Provisionally included here is the Glaeier Bay water shrew *(S. alaskanus)* (Hall, 1981), known only from two specimens taken at Point Gustavus, Glacier Bay, Alaska (Jaekson, 1928).

Pacific Shrew *(Sorex pacificus)*. This large, light brown shrew is restricted to the Pacific Coast coniferous forests from the eentral

Oregon coast (Siletz River) and Cascades (Crescent Lake) south to the Siskiyou Mountains of northern California in the interior, and along the Coast ranges to San Francisco Bay (Fig. 27). Throughout this range it exists with the much smaller *S. vagrans,* but unlike *vagrans, pacificus* lacks a medial tine on I1. It may be separated from *S. trowbridgii* on the basis of color and the absence of the post-mandibular canal in *pacificus;* from *S. bendirii* and *S. palustris*

FIG. 26.—Distribution of *Sorex palustris* (incl. *S. p. alaskanus*), *Sorex sclateri,* and *Sorex saussurei.*

by color and absence of medial tines on I1 in *pacificus* (see above). In the zone of potential contact between *S. pacificus* and *S. monticolus* (see below) in west-central Oregon, the situation is confusing. This zone runs from Lincoln and Taft, Lincoln Co., through Corvallis and Philomath, Linn Co., and Vida, Lane Co., to the crest of the Cascades. *S. monticolus bairdii,* smaller, darker, and with well-developed medial tines on I1, occurs north of this zone; to the south

Fig. 27.—Distribution of *Sorex monticolus* and *Sorex pacificus.*

is *S. pacificus,* larger, lighter, with no medial tines. However, some individuals in the zone of contact are large and light brown, but have distinct medial tines, suggesting some hybridization may be occurring (Hennings and Hoffmann, 1977). Further study of this situation is warranted.

Vagrant Shrew *(Sorex vagrans).* This shrew has a distribution centering on the Columbia Plateau, Snake River Plains, and northern Great Basin, but extending westward to the Pacific Coast, and eastward to the Continental Divide (Fig. 28). It is a small to medium-sized shrew whose most trenchant character is the unique pattern of the medial tine on the first incisor—pigmented, but high on the incisor and separated by an unpigmented area (Fig. 9a). Wherever it occurs with the slightly larger *S. monticolus* it is separable by this character, along with the greater interorbital breadth and longer palate of *S. monticolus* (Hennings and Hoffmann, 1977). The vagrant shrew lives in a variety of habitats—forest, meadow, and riparian—but they are ordinarily mesic. Another small *Otisorex* shrew, *S. preblei,* also occurs in much of the range of *S. vagrans,* but is adapted to more xeric conditions; *S. preblei* is smaller, and like its larger relative, *S. cinereus,* can be distinguished from *vagrans* and *monticolus* (in which U3 is smaller than U4), by the third unicuspid being larger than the fourth (rarely subequal). This pattern also distinguishes the smaller *S. lyelli* in the central Sierra Nevada. *S. palustris, S. bendirii,* and *S. pacificus* are all larger than *vagrans; S. merriami* is slightly smaller and, like *S. trowbridgii* on the Pacific Coast, in the subgenus *Sorex.* Along the east slope of the Sierra Nevada, and possibly in some of the Great Basin ranges occupied by *vagrans, S. tenellus* may occur; it is smaller and with a different medial tine pattern (see below).

Sorex vagrans also occurs in areas inhabited by members of the *S. ornatus* group, which have a small incisor tine pigmented like that of *monticolus* (Fig. 9c). Around San Francisco Bay, a complex and poorly understood situation exists. *S. ornatus californicus* occurs in the uplands surrounding the bay. The salt marsh habitat fringing the bay is occupied by darker individuals of two species; the "South Bay" (San Francisco Bay proper) from the Golden Gate around to San Pablo, supports *S. vagrans halicoetes,* while the salt marshes of the "North Bay" (San Pablo, Suisun bays) from Martinez to Tolay Creek are occupied by *S. ornatus sinuosus.* Populations of *S. o. sinuosus* in the Sacramento/San Joaquin river delta are nearly black, which originally led to their naming as a distinct species. However, populations of *S. v. halicoetes* from north of San Jose are equally dark. Jackson (1928) reported a very dark specimen of *S. v. vagrans* from salt marsh habitat on Lopez Island, San Juan Co., Washington, and *S. cinereus nigriculus* is a melanistic population known only from a salt marsh at Cape May, New Jersey (Green,

1932); salt marsh melanism in shrews deserves further investigation.

Rudd (1955) described some salt marsh shrews from the north shore of San Pablo Bay (Tolay Creek) as hybrids between *S. (o.) sinuosus* and *S. v. vagrans* on the basis of intergradation in color and external measurements; however, skulls of these shrews are for the most part typical of *ornatus* in medial tine pattern of the first incisor. Subsequently, Brown (1970) showed that all of the sup-

FIG. 28.—Distribution of *Sorex vagrans, Sorex longirostris* (incl. *S. l. fisheri*), and *Sorex oreopolus*.

posed hybrid populations exhibited karyotypes typical of *S. ornatus.* Both *vagrans* and *ornatus* occur in the vicinity of Petaluma and north of San Rafael without evidence of interbreeding. Salt marsh populations of both species *(S. ornatus salarius, S. vagrans paludivagus),* seem to occur on the peninsula south of San Francisco and south to Monterey Bay, but the taxonomy of the shrews in this area is unclear. At present, the best character for separating the two species is the nature of the medial tine on I1. The position of the foramen magnum and degree of flattening of the braincase, advocated by Jackson (1928), are too variable within either species to be of use.

Southeastern Shrew *(Sorex longirostris).* This small shrew is inappropriately named; it has one of the shortest rostra of North American *Sorex* (Fig. 10). The short, relatively broad rostrum, flattened braincase, distinctive medial tine on I1, and short tail (less than 31 mm) distinguish it from other *Otisorex* shrews in the southeastern United States. *S. dispar* and *S. fumeus* are much larger in cranial and external dimensions. *Sorex cinereus* is somewhat larger, has a relatively long, slender rostrum, higher braincase, and longer tail (more than 31 mm), and usually has U3 larger than U4. In *S. longirostris,* U3 is usually smaller than U4, or at least subequal, but individual exceptions occur in both species. At the northern edge of its range, *S. longirostris* may meet or overlap with *S. fontinalis,* a small member of the *cinereus* group with a relatively short rostrum and flattened skull (see below). However, the characters which separate *cinereus* from *longirostris,* though reduced in magnitude, still hold. Its geographic range is also shared by the much larger *S. palustris* and the much smaller *S. hoyi.* A population of shrews from the Great Dismal Swamp on the Virginia-North Carolina border, named *S. fisheri* by Merriam (1895), has long been regarded as a subspecies of *S. longirostris.* These shrews are much larger, with longer, relatively narrow rostra, and intergradation between *fisheri* and typical *longirostris* is not evident. The status of this population should be investigated.

Montane Shrew *(Sorex monticolus).* This is a medium-sized shrew, like *S. vagrans* rather variable geographically, but consistently larger where the two are sympatric. The montane shrew is well named in that it occurs mostly in the mountains of western North America, from northern Alaska to northern Mexico, although its range also extends eastward in the boreal taiga and northern Great Plains to at least north-central Manitoba (Wrigley, *et al.,* 1979) (Fig. 27). It shares most of its northern range with the small *S. hoyi* and the two usually tricolored subgenus *Sorex* shrews, *S. arcticus* and *S. tundrensis,* whose sizes overlap that of *monticolus,* but in which U3 is larger than U4. *S. trowbridgii* is about the same

size as *monticolus* where the two co-occur on the Pacific Coast, and both have U3 smaller than U4, but the concolored *trowbridgii* is also a subgenus *Sorex* shrew with well-developed post-mandibular canals, which *monticolus* lacks. The montane shrew is sympatrie with a fourth subgenus *Sorex* shrew of similar size in the southern Rockies, *S. arizonae,* which, however, has U3 larger than U4.

As indicated above, *S. monticolus* is best separated from *S. vagrans* by the medial I1 tine pattern (Fig. 9), greater interorbital breadth and palatal length, as well as slightly larger size (skull and toothrow length). *S. cinereus* and *S. preblei* are both smaller, and U3 is larger than U4. *S. bendirii* is much larger, as is *S. palustris,* and both have distinctive color patterns (see above). Shrews of the *S. ornatus* group share with *S. monticolus* the same medial tine pattern on I1, U3 usually smaller than U4, and the lack of post-mandibular canals. Of this group, *S. nanus* and *S. tenellus* are markedly smaller than *monticolus; S. ornatus,* however, overlaps *monticolus* in size. Fortunately, the ranges of the two species are mostly separate. The zone of potential contact or overlap exists along the west slope of the Sierra Nevada, from Yosemite south to the San Bernardino Mountains. In this region, *S. monticolus* is slightly larger than *S. ornatus* in any one locality, with a more inflated braincase and more crowded toothrow (Figs. 11, 12). *Sorex durangae,* described from El Salto, Durango, Mexico, is a synonym of *S. monticolus* (Hennings and Hoffmann, 1977).

Ornate Shrew *(Sorex ornatus).* Means by which this species can be separated from the *Otisorex* shrews that most closely resemble it, *S. vagrans* and *S. monticolus,* have been discussed above. It may be distinguished from *S. trowbridgii* by its smaller size and lack of post-mandibular foramina, as well as by the Trowbridge shrew's distinctive color pattern. *S. ornatus* is most similar to *S. tenellus,* which is slightly smaller, and with paler pelage. The two species are thought to be allopatric, separated by the Owens Valley, but the relationships between the two are unclear. Provisionally included here with *S. ornatus* are several populations that have in the past been given specific status. *Sorex o. sinuosus* is a melanistic population in the delta of the Sacramento/San Joaquin River, and along the north shore of San Pablo Bay (see *S. vagrans); S. o. willeti* is known from the holotype only, taken from Santa Catalina Island (Von Blocker, 1967); *S. o. juncensis* is known from only two specimens, geographically adjacent, that in color and cranial morphology resemble *S. ornatus* (Hall, 1981). *Sorex trigonirostris,* from Ashland, Jackson Co., Oregon, was described as a species in the *S. ornatus* group, but is a synonym of *S. vagrans* (Hennings and Hoffmann, 1977).

Dwarf Shrew *(Sorex nanus).* This small species shares the medial tine pattern on I1 with *S. monticolus* and *S. tenellus;* U3 is also smaller than U4, but *nanus* is smaller in size than either species. There are no unequivocal characters to separate *nanus* from *tenellus,* but they are not presently known to come in contact with each other (Hoffmann and Owen, 1980). *S. nanus* can be distinguished from members of the *cinereus* group *(cinereus, preblei,* and *haydeni)* by the relative sizes of the third and fourth unicuspids. Since their geographic ranges overlap, it may come in contact with either *S. vagrans,* from which it may be distinguished by the I1 medial tine pattern, or the more xerically-adapted *S. merriami,* a member of the subgenus *Sorex,* which has no medial incisor tine. It may also be sympatric with *S. palustris* and *S. hoyi.*

Inyo Shrew *(Sorex tenellus).* There are no other species of *Otisorex* known to occur within the limited range of this species (Fig. 25); the only other shrew likely to be encountered in its arid habitat is *S. merriami,* which lacks the medial tine on I1 and has U3 larger than U4.

Smoky Shrew *(Sorex fumeus).* The smoky shrew is restricted to the northeastern United States and adjacent Canada (Fig. 31), where it occupies the floor of mixed deciduous-coniferous forest and taiga. It shares this habitat with *S. dispar* and *S. gaspensis* (see above), as well as with the smaller *S. cinereus, S. fontinalis,* and *S. hoyi,* and the larger *S. palustris.* It is most likely to be confused with *S. arcticus,* since both occur in southern Ontario, New Brunswick, and Nova Scotia, and overlap in size. The smoky shrew is uniform in color on back, sides, and belly, whereas *S. arcticus* is usually "tricolored" (see below). In the area of sympatry, *S. fumeus* is the smaller of the pair, and its skull is usually relatively flat (Fig. 15), while that of *arcticus* is more inflated, although some overlap may occur. Moreover, the arctic shrew is a member of the subgenus *Sorex* and thus possesses well-developed post-mandibular foramina, and lacks the pigmented ridge on the unicuspids. While *S. fumeus* seems to be an *Otisorex* shrew, individuals have a higher frequency of post-mandibular foramina on one, and sometimes both sides, than is true of most members of the subgenus, and the ridge on the unicuspids is not as well developed nor as heavily pigmented as typical *Otisorex;* individual *S. fumeus* may thus be sometimes confused with subgenus *Sorex* shrews.

Preble Shrew *(Sorex preblei).* This is an extremely small shrew, approaching *S. nanus* and *S. hoyi* in size. It is found in arid and semiarid habitats from the Columbia Plateau to the northern Great Plains (Fig. 29), but has rarely been caught, and until recently was thought to be allopatric in distribution relative to other members of the *cinereus* group (Hoffmann, *et al.,* 1969). It can be distinguished

from *S. vagrans* and *S. nanus* by having U3 larger than U4; it shares this character with *S. cinereus* and *S. haydeni*. *S. preblei* (Fig. 17) can be distinguished from *S. cinereus* by its considerably smaller size, relatively flatter skull, and broader rostrum. It is very difficult to separate *S. haydeni* from *S. preblei* except by direct comparison of the two species at a single locality, where *preblei* appears to be consistently slightly smaller (Hoffmann, *et al., op. cit.;* Hoffmann and Fisher, 1978).

Pribilof Shrew *(Sorex hydrodromus).* This insular species is confined to St. Paul Island, of the Pribilof group in the Bering Sea. It was once regarded as close to the *arcticus* group (Jackson, 1928; Hall, 1959), but is now thought to belong to the *cinereus* group (Hoffmann and Peterson, 1967). The name is based on two specimens reported to have come from "Unalaska." This was interpreted as referring to Unalaska Island, but no shrews have subsequently been found there. The locality probably refers to the Unalaska District, which at the time the shrews were collected included the Pribilof Islands (Hoffmann and Peterson, *op. cit.). Sorex pribilofensis,* a junior synonym, was subsequently described from the Pribilof Islands.

St. Lawrence Shrew *(Sorex jacksoni).* Like the previous species, *S. jacksoni* is confined to an island in the Bering Sea, a remnant of the wide land connection that formerly existed between eastern Siberia and western Alaska during the last glacial period, when sea level was much lower. *S. jacksoni* is also a member of the *cinereus* group (Hoffmann and Peterson, 1967), although formerly regarded as a member of the *arcticus* group (Hall and Gilmore, 1932). It is the only shrew on St. Lawrence Island.

Hayden Shrew *(Sorex haydeni).* Another small shrew of the *cinereus* group, *S. haydeni* was until recently regarded as a subspecies. Van Zyll de Jong (1980) presented evidence, however, that *cinereus* and *haydeni* act as distinct species in the northern part of the zone of contact. We therefore treat *cinereus* and *haydeni* as separate species. *S. haydeni* has a relatively shorter unicuspid toothrow and wider breadth between the buccal edges of the second molars; plots of this ratio are disjunct and have been used in the key. *S. haydeni* skulls are flatter than those of *cinereus,* and have shorter rostra (Figs. 16, 18). Tails of *haydeni* are shorter and have a lighter tuft on the end than do those of *cinereus. S. preblei* resembles both *cinereus* and *haydeni,* but it is always smaller than either when in sympatry.

Along the northern edge of its range (Fig. 30), *S. haydeni* is sympatric with *S. cinereus* in several places, but it is usually found in grassy habitats, whereas *S. cinereus* prefers forest and woodland (Van Zyll de Jong, *op. cit.*). The western border of its range is

FIG. 29.—Distribution of *Sorex arcticus, Sorex tundrensis,* and *Sorex preblei.*

roughly coneordant with the eastern outliers of the Rocky Mountains, but the nature of its eontact and/or overlap with *S. cinereus* there has not been studied. To the east, in Minnesota and perhaps Iowa, *S. haydeni* may also be parapatric or sympatrie with *S. cinereus.* Here the situation is further eomplicated by the presence of similar small shrews along the southern edge of the range of *cinereus,* many of whieh have traditionally been assigned to subspecies

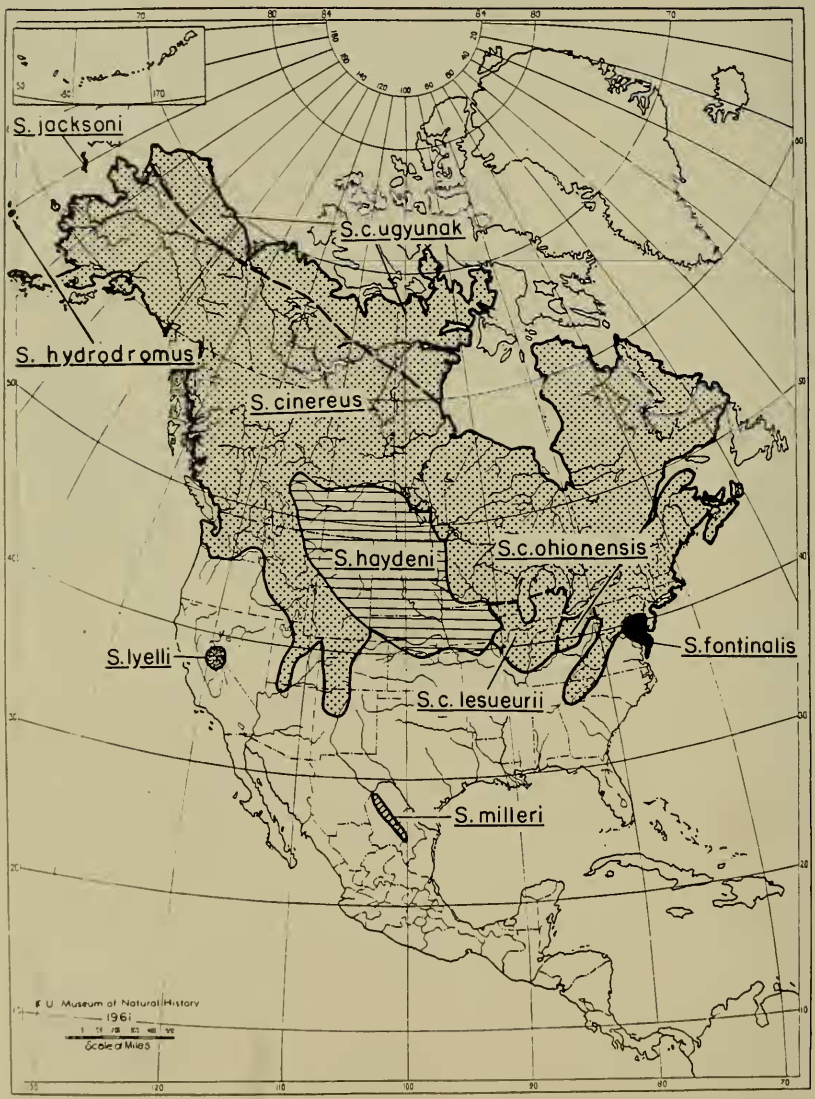

FIG. 30.—Distribution of *Sorex cinereus (S. c. cinereus ssp., S. c. ugyunak, S. c. lesueurii, S. c. ohionensis), Sorex fontinalis, Sorex haydeni, Sorex lyelli, Sorex milleri, Sorex hydrodromus,* and *Sorex jacksoni.*

of *S. cinereus: S. c. lesueurii* and *S. c. ohionensis.* The relationships of these populations to *S. haydeni* and *S. fontinalis* (see below), as well as to *cinereus* proper and *longirostris* need further study.

Maryland Shrew *(Sorex fontinalis).* This small member of the *cinereus* group has been regarded as a subspecies. However, Kirk-

land (1977) has recently demonstrated that *fontinalis* and *cinereus* overlap without intergrading in southeastern Pennsylvania. Here *fontinalis* is smaller, with a relatively shorter, broader rostrum, and shorter unicuspid toothrow, though not to the extent seen in *S. haydeni*. Compared to *cinereus* the skull of *fontinalis* is relatively flat. The relationship of *fontinalis* to *haydeni* and other small *cinereus* group shrews with short rostra needs further study.

Lyell Shrew *(Sorex lyelli).* This rarely-captured allospecies of the *cinereus* group has been found only at high altitudes (above 2000 m—about 6000 ft) in the central Sierra Nevada of California (Fig. 30). It may be told from other *Otisorex* shrews in this region *(ornatus, vagrans, monticolus),* as well as from *S. trowbridgii,* by having U3 larger than U4.

Masked Shrew *(Sorex cinereus).* This species has the largest range of any North American *Sorex,* and is quite variable geographically. Its main range is in the transcontinental coniferous forest, with extensions southward in montane forests of the Appalachians and Rocky Mountains, but it also occurs northward into the tundra, and in mixed and deciduous forest and woodland along the southern margin of the range (Fig. 30). Because of its large range, it occurs in sympatry with more species than any other North American *Sorex.* Suggestions for distinguishing *cinereus* from other species may be found in these accounts: *arcticus, tundrensis, vagrans, longirostris, monticolus, nanus, dispar, gaspensis, fumeus, preblei, haydeni,* and *fontinalis.*

Most populations of *S. cinereus* have a skull length of 15.0-16.5 mm, and U3 larger than U4. The relative size of these unicuspids separates *cinereus* from *monticolus, vagrans, longirostris,* and *nanus.* In cases where the unicuspid relationships are the same, *arcticus* and *tundrensis* (both subgenus *Sorex), dispar* and *fumeus* are larger (CB length $>$ 16.4 mm) and *preblei* is smaller (CB length $<$ 14.7 mm).

Individuals in a few populations of *cinereus* exceed 16.5 mm in skull length (*S. c. streatori* of the northwestern Pacific Coast, to 17.0; *S. c. miscix* of Labrador and *S. c. acadicus* of Cape Breton Island and Nova Scotia, to 16.8 mm). In most cases this does not cause problems of identification, except on Cape Breton Island and Nova Scotia where these large *S. cinereus* are sympatric with *S. gaspensis* and *S. fumeus,* respectively, and may be confused. Of the three, *fumeus* is largest, with a broad rostrum (maxillary breadth $>$ 4.6 mm); *gaspensis* is smallest and has a very long tail (45-55 mm) and narrow rostrum (maxillary breadth $<$ 4.0 mm); and *S. c. acadicus* is intermediate in these characters (maxillary breadth 4.0-4.4 mm, tail $<$ 46 mm).

Other populations of *S. cinereus* are smaller than 15.0 mm in

skull length. *S. c. ugyunak* ranges in tundra habitats across northern Alaska to Hudson Bay. Its skull length is 14.1-15.5 mm, but the only other shrews in this area are the much larger subgenus *Sorex* shrews, *S. arcticus* and *S. tundrensis*, with which *S. c. ugyunak* shares a "tricolor" pelage (see Bee and Hall, 1956; frontispiece). Van Zyll de Jong (1976b) reports that *S. c. ugyunak* is closer in cranial morphology to *S. hydrodromus, S. jacksoni,* and *S. haydeni* than it is to other populations of *S. cinereus;* study of the zone of potential contact between *ugyunak* and *cinereus* spp. is needed.

S. cinereus along the southeastern edge of the species range *(S. c. lesueurii, S. c. ohionensis)* have been discussed under the account of *S. haydeni*. Not only are some individuals unusually small (skull length 14.6-15.9 mm), but in some *ohionensis,* U3 is often smaller than U4 (Bole and Molthrop, 1942). Some of these populations may eventually prove to be referable to *S. haydeni,* to *S. fontinalis,* or perhaps even to *S. longirostris.*

Subgenus *Sorex*

Trowbridge Shrew *(Sorex trowbridgii).* This species is confined to the coniferous forests of the Pacific Coast, ranging eastward to the east slopes of the Cascade Mountains and Sierra Nevada (Fig. 31). It is a fairly large, dark colored shrew, with venter nearly as dark as dorsum, but with a sharply bicolored tail, dark above and light below. Cranially, it is distinguished from other Pacific Coast *Sorex* by its combination of U3 smaller than U4, small medial tine on I1, and presence of post-mandibular foramina. It occurs with *S. vagrans, S. monticolus, S. pacificus, S. ornatus, S. palustris,* and *S. bendirii,* all *Otisorex* shrews which lack well-developed post-mandibular foramina. In southeastern Oregon and northwestern California, its range may overlap that of another shrew of the same subgenus, *S. merriami* (see below), but *merriami* does not have a medial tine on I1 and its U3 is larger than U4. The habitats of the two also differ, *S. trowbridgii* being primarily a woodland species, whereas *S. merriami* inhabits xeric steppe and desert.

Merriam Shrew *(Sorex merriami).* This shrew is one of the most xeric-adapted of all North American *Sorex*. It has been taken in scattered localities in the Great Basin and Columbia Plateau, and probably inhabits sagebrush desert and shrub steppe throughout this region. It also occurs in the northern Great Plains and southern Rocky Mountains (Fig. 31). Within its range it is the only species of the subgenus *Sorex*, except along the east slope of the Cascades and Sierra Nevada, where it may come in contact with *S. trowbridgii* (see above). In the southern Rockies, *S. arizonae* is known from southeastern Arizona and southwestern New Mexico, and while the two species presently are considered allopatric, their

ranges may be found to come into contact or overlap. *S. arizonae* (see below) has a medial tine on I1, which *merriami* lacks, as well as a narrower palate (Diersing and Hoffmeister, 1977). The only *Otisorex* shrews likely to be taken in the same places as Merriam shrews are the much smaller *S. nanus*, *S. tenellus*, and *S. preblei*, from which *S. merriami* can be easily distinguished by its paler

FIG. 31.—Distribution of *Sorex fumeus*, *Sorex trowbridgii*, *Sorex merriami*, *Sorex arizonae*, *Sorex emarginatus*, *Sorex ventralis*, and *Sorex stizodon*.

color, well-developed post-mandibular canal, U3 larger than U4, lack of medial tine on I1, and broad palate.

Arizona Shrew *(Sorex arizonae).* This species was described only recently (Diersing and Hoffmeister, 1977) and is presently known only from the Huachuca, Santa Rita, and Chiricahua mountains of southeastern Arizona, the Animas mountains of southwestern New Mexico (Conway and Schmitt, 1978), and the Sierra Madre Occidental of Chihuahua, Mexico (Caire, *et al.*, 1978) (Fig. 31). It may occur with *S. merriami* (see above), and the *Otisorex* shrew *S. monticolus,* which may be distinguished by subgeneric characters and by having U3 smaller than U4. *Sorex emarginatus,* known from Durango, Jalisco, and Zacatecas, Mexico (see below), is also a subgenus *Sorex* shrew, and is closest to *S. arizonae* (Diersing and Hoffmeister, 1977). *S. emarginatus* is not referable to *S. oreopolus* (Findley, 1955b), which is a member of the subgenus *Otisorex* (Diersing and Hoffmeister, *op. cit.*).

Arctic Shrew *(Sorex arcticus).* This large shrew, usually distinguishable by its distinctively "tricolored" coat pattern, inhabits the transcontinental northern coniferous forest or boreal taiga from Nova Scotia and Quebec westward to the central Yukon (Fig. 31). It is replaced in the western Yukon and Alaska by the similar *S. tundrensis,* which until recently (Youngman, 1975) was considered conspecific with *S. arcticus.* Throughout this entire region, the arctic shrew is the only member of the subgenus *Sorex,* and may be distinguished from *Otisorex* shrews that occur in the same area by its well-developed post-mandibular canals, lack of pigmented ridges on the unicuspids, and externally, by its light sides, which usually contrast strongly with the dark back, especially in winter pelage (juveniles in summer pelage are at best, faintly tricolored).

In southern Ontario, the range of *S. arcticus* overlaps that of *S. fumeus,* in which the pigmentation of the unicuspid ridges is often weakly developed, and in which a post-mandibular canal is sometimes present, at least on one side. However, *S. fumeus* is smaller (maxillary toothrow less than 6.6 mm, compared to more than 6.7 mm for *S. arcticus*), and externally it lacks the light sides of *S. arcticus.* In northern Canada and Alaska (Fig. 31), *S. arcticus* occurs with populations of *S. cinereus* that may have distinctly lighter sides, but these individuals are much smaller and lack post-mandibular canals. In the western part of its range, *arcticus* also occurs with *S. monticolus,* which has U3 smaller than U4.

Tundra Shrew *(Sorex tundrensis).* This large "tricolored" shrew replaces *S. arcticus* in the boreal taiga of the western Yukon, extreme northwestern British Columbia (Nagorsen and Jones, 1981) and Alaska, and probably also occurs extensively in eastern and central Eurasia, where it is usually referred to as *S. arcticus* (cf.

Corbet, 1978). The ranges of *tundrensis* and *arcticus* are nowhere in contact, as far as is now known, but in any case, the two species can be separated by size and nature of the upper unicuspid teeth (see Key; Fig. 23). The tundra shrew can be distinguished from shrews of the subgenera *Microsorex* and *Otisorex* by the same characters which will separate *S. arcticus* (see above).

Middle American *Sorex*

Although the Mexican and Guatemalan *Sorex* have not been included in the Key, pending revision, some discussion of these shrews is appropriate here.

Subgenus *Otisorex*

Verapaz Shrew *(Sorex veraepacis)* and **Large-toothed Shrew** *(Sorex macrodon).* These are very large members of the subgenus *Otisorex,* rivaling *S. pacificus* and *S. fumeus* in size. They occur in montane forests from central Guerrero, Puebla, and Veracruz, Mexico, south through the highlands of Oaxaca and Chiapas, Mexico, to southwestern Guatemala (Fig. 24). They lack post-mandibular foramina, have pigmented ridges on the unicuspids, and U3 is smaller than U4. The medial tines of the first incisors are well-developed, but not heavily pigmented, and are rather high on the face of the incisor. *S. macrodon* and *S. veraepacis* are similar in morphology and allopatric in distribution; further collecting may demonstrate that they are conspecific.

Miller Shrew *(Sorex milleri).* This species is restricted to the Sierra Madre Oriental of Coahuila and Nuevo Leon, Mexico (Fig. 30). It is of moderate size, with a narrow rostrum and inflated braincase; the third unicuspid is larger than the fourth. The post-mandibular foramina are sometimes present, but are variable in size and occurrence; in many specimens examined, they are absent. The species is tentatively assigned to the subgenus *Otisorex,* in the *cinereus* group, as suggested by Findley (1955a, b).

Volcano Shrew *(Sorex oreopolus).* This medium-sized shrew has long been confused with two other Mexican taxa, *emarginatus* and *ventralis.* Findley (1955b) combined them under this oldest name, but the holotype of *oreopolus* is an *Otisorex* shrew, whereas *emarginatus* and *ventralis* belong to the subgenus *Sorex* (see below) (Diersing and Hoffmeister, 1977; Hoffmann, in prep.). *Sorex vagrans orizabae* has also been described from the Transverse Volcanic Belt, and appears to be very similar to *S. oreopolus* (Hoffmann, in prep.); it is therefore provisionally placed in synonymy with the older name. The volcano shrew occurs at high elevations from extreme southwestern Jalisco (type locality of *oreopolus*) to eastern Puebla (type locality of *orizabae*) and western Veracruz (Fig. 28). *S.*

saussurei (see below), a larger member of the subgenus *Sorex,* is sympatric with *oreopolus* in this area, but has well-developed post-mandibular foramina. *S. oreopolus* is not known to be sympatric with the two smaller subgenus *Sorex* shrews, *S. emarginatus* and *S. ventralis* (see below).

Subgenus *Sorex*

Saussure Shrew *(Sorex saussurei).* This species, as presently understood, is the most widespread and geographically variable shrew in Middle America (Fig. 26). It occurs from southern Coahuila and Durango, Mexico, south to at least central Oaxaca. South of the Isthmus of Tehuantepec, in central Chiapas, Mexico, and in southwestern Guatemala other populations occur that are provisionally retained in *S. saussurei* although they may eventually be shown to be closer to *S. ventralis* or else specifically distinct. The Saussure shrew has a well-developed post-mandibular foramen, and the medial tines on the first incisor are well developed and pigmented. The unicuspids lack pigmented ridges, and the first and second are subequal in size, the second often somewhat larger than the first; the third and fourth are also subequal, but markedly smaller than the first two. *S. saussurei* is sympatric with *S. oreopolus* and *S. veraepacis* (see above), and may also contact the southern ends of the ranges of *S. monticolus* and *S. milleri;* all of these species may be distinguished as *Otisorex* shrews. The relationship of *saussurei* to the smaller subgenus *Sorex* shrews of Mexico *(emarginatus, ventralis)* is confused. So far, they seem separable only on the basis of size, with little or no overlap between large and small taxa (CB length; *saussurei* $>$ 17.4 mm, *emarginatus* and *ventralis* $<$ 17.4 mm). Moreover, each of the allopatric small taxa co-occur with the large *saussurei,* but not with each other (*i.e., saussurei* and *ventralis* at Huachinango, Puebla; *saussurei* and *emarginatus* near Autlan, Jalisco).

Cerro San Felipe Shrew *(Sorex ventralis).* As discussed above, this is a small member of the subgenus *Sorex,* and is not conspecific with *S. oreopolus.* It is known to occur from central Oaxaca north to northwestern Puebla (Fig. 31). Where it is sympatric with *S. saussurei* and *S. veraepacis,* it can be distinguished on the basis of size. From *S. oreopolus,* if they should prove to be sympatric, it can be told by its U3 subequal to or larger than U4, and the presence of a post-mandibular foramen. Its distribution seems to be allopatric to that of the very similar *S. emarginatus* (see below).

Zacatecas Shrew *(Sorex emarginatus).* Like the previous species, this one has also been erroneously considered conspecific with *S. oreopolus.* It is a small (CB length 16.4-16.9 mm) member of the subgenus *Sorex,* occurring from southwestern Durango through